The research presented in this thesis was carried out by myself, with the exception of the work discussed in Chapter 13. This latter experiment was carried out jointly with Dr. Hamish MacLeod.

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AGGRESSIVE MOTIVATION AND REINFORCEMENT IN THE SIAMESE FIGHTING FISH(BETTA SPLENDENS).

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ABSTRACT

This thesis describes operant behaviour rewarded by aggressive display in Betta splendens. Withdrawals during the encounters were related to the phase of the nest-building cycle, although not to the presence of the nest. Subordinates elicited more withdrawals than displaying males. Withdrawal is here interpreted as courtship, which was inhibited if the partner displayed aggressively, and sex discrimination in Betta splendens is discussed.

Measures of behaviour during reinforcement were correlated with one another and with behaviour between reinforcements. One group of post-reward behaviour patterns delayed further operant responses. During reward, some behaviour patterns (e.g. attack, air gulping) were associated with short, and others (e.g. lateral display) with long operant latencies. With the exception of air gulping, these relations could be accounted for in terms of relations to post-reward behaviour patterns. A second group of post-reward behaviour patterns, negatively related to the first, did not delay operant performance and was positively related to attack during reinforcement. Priming with aggressive display changed behaviour during the reward and decreased operant latency. This could not be accounted for by changes in post-reward behaviour.

Increasing the interval between stimulus presentations (IPI) decreased attack and increased lateral display duration. Attack decreases operant latencies, but the existence of a latent period in turn reduces attack (the mechanism involves decay of stimulus-induced excitation in the period when the stimulus is absent, i.e. the inter-reward interval). Two procedures which increase this interval decreased response rate: a time-out of 30 or 60 mins. after training reduced the number of responses in extinction by 50% approximately, whilst a fixed ratio (FR) schedule reduced response rate and eliminated the intra-session acceleration in responding which occurred under continuous reinforcement.

In a free-behaviour situation with food-rewarded doves, meal size first increased and then decreased as FR was increased. (Body weight was maintained by changes in feeding efficiency and meal frequency). Accompanying the meal-size changes, there were changes in anticipatory feeding (changes in the correlation between meal size and the post-meal interval) and in an index of intra-meal facilitation of feeding. Many of these effects depended on facilitatory effects of feeding which decayed during the inter-reward interval. Increasing FR size increased this interval, and reduced persistence in meals.

Contents

CHAPTER 1

1.1 Introduction

The Siamese fighting fish (Betta splendens) will learn to perform an instrumental response for the opportunity to display aggressively (Thomson, 1963; Hogan, 1967). These and other experiments using unconventional reward procedures have become central in stimulating reconsideration of the problem of reinforcement and it's control of behaviour. The research reported in this thesis attempts to discover some of the motivational processes underlying display reward in Betta splendens and determine the nature of the relations between display and the operant behaviour it reinforces. It is hoped that a detailed investigation of this reward type will help in the understanding of reward processes by revealing aspects of this particular system whose nature can be compared with those underlying operant performance for other rewards.

1.2 Reinforcement As An Operation

Since the learning studies of Thorndike (1911) most attempts to describe the conditions necessary to produce learning in animals have included description of a reward or reinforcement procedure. A procedure is considered reinforcing if, when it is made contingent on some behaviour of the animal, the frequency of occurence of that behaviour increases (after Skinner, 1938).

The range of procedures which can act as reinforcers is enormous. It includes the administration of food, water, oxygen, heat and various drugs to animals who have been appropriately deprived; the opportunity to engage in species specific behaviours, such as nest building, digging, grooming, hoarding, gnawing and running, and the opportunity to engage in social activities such as aggressive display, sexual behaviour, hearing conspecific bird song, interacting with an imprinting stimulus and pup retrieving. Other less 'natural' rewards include electrical stimulation of certain areas of the brain and almost any stimulus change at all if the animal is kept in a relatively constant environment. These findings

will not be treated in detail here, since comprehensive reviews of this literature have been carried out by Tapp (1969) Glickman (1973) Bolles (1975) and Hogan and Roper (1978). In it s operational sense, reinforcement is a set of procedures enlarged empirically (Skinner, 1938).

1.3 Reinforcement As A Principle

The question of why these procedures produce learning and support the continued performance of the learned response, has been traditionally answered by invoking a principle of reinforcement. As used by Thorndike (1911) the principle of reinforcement took the form of the Law of Effect (p. 244) which was, along with the Law of Exercise, intended to

> "give an account of a wide range of experience, so long as all that is demanded is a rough and general means of prophecy". (p.245)

According to Thorndike any set of procedures which leads to a "satisfying" state or terminates an "annoying" state for the animal will, if made contingent on its behaviour, result in learning. Despite Thorndike's operational definition of satisfiers and annoyers (1911, p. 245) the subjective overtones of the terms he chose to use were unacceptable to the behaviourists of the following decades. As a result, the reflex theory of Watson (1925) based on Pavlov's (1906) conditioned reflex concepts, could not adequately account for instrumental learning. It remained for Skinner (1938) to put forward a stimulus-response view of behaviour which had a place for reinforcements and their effects, and which formulation a principle of reinforcement plays a major role.

1.4 Reinforcement As a Unitary Process

The nature of the reinforcement principle has traditionally been assumed to be unitary. Whatever it s mode of action, tissue-need reduction (Hull, 1943) drive reduction (Miller, 1951) or related to the consummatory response (Sheffield, Roby and Campbell, 1954) it was the same process for all reward types,

and affected all responses in the same way.

This is part of what Seligman (1970) terms, " the assumption of equivalence of associability", which is, that all responses can be associated equally well with all stimuli, including reward stimuli. This assumption determined, and was determined by, three major factors.

a) Learning studies used only a restricted range of species, most studies using the rat or the pigeon. This was not entirely a matter of convenience. It was partly attributable to the conviction that the most rapid progress in understanding behaviour would result from concentration on a small number of "representative" species (Skinner, 1938). In spite of Beach's (1950) criticism of the idea of a representative species and of the Norway Rat's qualifications for such a role (c.f. Breland and Breland ,1961 and Whalen, 1961) a wider range of species has only recently been used in learning studies.

b) Only a small number of learning situations were commonly used, most often the Skinner boxes or mazes. Again, this was not entirely due to their convenience. Instead, their use grew from the acceptance of the premise that most information about laws of behaviour would be gained from the study of arbitrarily chosen, rather than naturally occurring events. Thus the bar-press, because it is foreign to the rat, will reveal regularities in performance reflecting general laws of learning rather than the animal's experience or natural propensities. Seligman (1970) points out that the danger of such a strategy is that, "the laws so found will not be general, but peculiar to arbitrary events". This must include laws relating reward and the performance characteristics of the learned behaviour.

c) Most studies of reinforcement used food, water or electric shock as rewards, but their findings were generalized to account for all other forms of reward. One possible reason for this generalization concerns traditional views of the nature of the motivational systems underlying the reinforcement event.

Woodworth (1937, p. 301) remarks,

> "Evidently reward and punishment would be impossible with a creature that had no preferences, no needs, no appetites or aversions",

and to Woodworth (1918) can be traced the distinction between the motivating and response selecting aspects of behaviour systems from which developed the view that all behaviour is the result of a general "drive" to activity. Functionally distinct activities, according to general drive theories, are all motivated from the same source, as is instrumental behaviour for all reward types. As Hebb (1955, p. 249) puts it,

> "Drive is an energiser but not a guide; an engine but not a steering gear."

In it's most influential formulation, Hull (1943)represented drive as being the summation of all specific need states with this sum controlling learned behaviour. (For criticism see Bolles, 1958; Hilgard and Marquis, 1961; Ziegler, 1964; McFarland, 1965). Even when drives or other causal factors are not viewed as general but specific to functionally related activities (e.g. Tinbergen, 1951) the unitary conception of motivation leads to the expectation that different reward types will control a learned behaviour in similar ways. Only recently has a view of motivational systems been advanced which explicitely argues that the achieving of different types of functional end points requires different types of motivational mechanism (Toates and Archer, 1978).

The laws of learning and performance resulting from a tradition in which the three above factors coexisted, have been subject to criticism on three major fronts:

1) It has been questioned whether all responses within the animals' repertoire are equally conditionable (e.g. Seligman, 1970; Shettleworth, 1975).
2) It has been shown that responses differ in their compatibility with certain reinforcers (e.g. Bolles, 1970; Sevenster, 1968, 1973; Stevenson-Hinde, 1973).
3) Comparisons have been carried out in an attempt to ascertain

Whether all reinforcers affect instrumental performance in the same way (reviewed by Hogan and Roper, 1978).*

It is in this last field of the comparison of the properties of different reinforcers that the Siamese fighting fish (Betta splendens) has become a species of interest to those working with the phenomena of learning and instrumental performance.

Since Hogan and Roper's review of this area is an exhaustive one, the present discussion will restrict itself to illustration of some of the central issues which have arisen from reinforcer comparisons. Most studies of reinforcement, and the review mentioned, do not consider the problem of learning per/se, but place most emphasis on examination of the patterns of performance of the learned behaviour. Some discussion of the basis for the learning distinction is required.

1.5 The Learning-Performance Distinction

The separation of learning and performance processes in accounting for the effects of conditioning procedures was proposed by Lashley (1929), (see also Skinner, 1938; Hull, 1943; Tolman, 1955; Hogan and Roper, 1978). The changes in behaviour for which these two sets of variables are considered responsible are not immediately distinguishable, their effects being separated by reference to their temporal characteristics (Hilgard and Marquis, 1961, p. 5). Whatever the precise nature of learning processes, a gradual process (e.g. Hull, 1943; Spence, 1945) or one acting after a single reward (e.g. Lashley, 1929; Guthrie, 1935; Skinner, 1938; Estes, 1950) these mechanisms produce a long-term change in behaviour. In contrast, performance variables such as motivation and fatigue are inferred to account for shorter-term changes. (But see Bindra, 1969, who makes no learning-performance distinction). The major questions currently asked about the reinforcement process concern the latter short-term phenomena, while little attention has been paid to possible differences in the aquisition of a response.

*I am indebted to Dr. J.A. Hogan for sending me a pre-print of this useful review.

1.6 Differences In The Properties Of Reinforcers

The recent increase in the number of species and reward types used in investigations of instrumental behaviour have led to questioning of the unitary nature of the reinforcement principle and the generality of "laws of learning". Since Hogan and Roper (1978) review in detail the performance characteristics of behaviour for a wide range of reward types, the present treatment will concentrate on a few reinforcers for which the evidence suggests performance differs from that for food reward. Furthermore, only two types of performance differences will be considered at first: resistance to extinction and fixed ratio compensation. Discussion will then centre on possible explanations for these reward differences. In a later section (ch.8.1) a third type of reinforcer difference will be discussed: the effect of varying the amount of reward.

1.61 The Rate Of Extinction:

1.61(a) Food And Water

Few experiments have directly compared the rate of extinction for different rewards. Macdonald and de Toledo (1974) compared performance in extinction for water and food rewarded rats. During training, two test situations were used, one involving lever pressing and the other alley running, and rats in both situations were rewarded continuously or intermittently. For both tasks, extinction was most rapid after water reward and water also produced a smaller partial reinforcement effect (see Mackintosh, 1974, p. 72). These results have been brought into question by the findings of Shanab, Melrose and Young, 1975; Seybert and Gerard, 1976; and Seybert, Gerard, Lawrence, Nash and Williams, 1976. These studies find a much stronger partial reinforcement effect for water reward. Nevertheless, despite this difficulty, Macdonald and Toledo's experiment is a direct comparison and it's results can be seriously undermined only by other comparative studies.

1.6(b) Heat

For heat reward, no direct comparison of the speed of

extinction after this and another reinforcer has been carried out. However, after food reward, resistance to extinction is positively related to Fixed Interval duration (the partial reinforcement effect). No such effect was found by Leeming (1968) for a rearing response in heat-rewarded rats. In addition resistance to extinction was positively related to amount of reward which is the opposite relation to that reported for food reward.

1.61 (c) Brain Stimulation

Direct comparisons have been made between resistance to extinction after reward by electrical stimulation of the brain (ESB) and by water. After experiments reporting unusually rapid extinction for ESB (e.g. Olds and Milner, 1954; Seward, Uyeda and Olds, 1959), Gibson, Reid, Sakai and Porter(1965) directly compared some of the properties of ESB and sugar-water rewards in rats. Pointing out that the spatio-temporal relation of ESB and the response usually differs from that of food and the response, they equalized this by using a situation in which a lever press had to be followed by licking a cup at which either ESB or sugar water was administered. In addition, a group of rats were trained to lick a cup without preceding it with a lever press, and were instantly rewarded with ESB or sugar water. The lever press group showed faster extinction than the cup group, but no reward difference emerged. In addition Olds (1956) found no extinction differences between rats maze running for food and ESB rewards. Quartermain and Webster (1968) used a lever incorporating a cup on it's upper surface to compare the resistance to extinction of rats trained with water reward and those trained with ESB. Half of the rats had a 30min. extinction session immediately after training, while the other half had a 1hr. "time-out" between the last acquisition trial and the beginning of extinction, during which they were returned to their home cages. All rats produced the same number of responses in extinction except for the ESB group with the 1hr. delay, which showed far fewer responses. ESB, food and water rewards seem, therefore, identical in their effects on resistance to extinction, except for the sensitivity of

ESB reward to delays (See Deutsch and Howarth, 1963; Gallistel, 1973 for review).

1.61 (d) Aggressive Display

Direct comparisons of resistance to extinction for food and aggressive display rewards have been made. Male Siamese fighting fish (Betta splendens) in a runway situation (Hogan, 1967) or with a ring-swimming operant (Hogan, 1978) extinguish more rapidly when previously rewarded by mirror induced aggressive display, than after sessions of food reward.

1.61 (e) Summary

After reviewing extinction differences in the properties of different reinforcers, Hogan and Roper (1978, p. 228) conclude,

> "In those cases in which a direct comparison has been attempted..., either no differences were found, or the differences were attributed to motivational factors..."

1.62 Fixed Ratio Performance

1.62 (a) Food

If an animal in a Skinner box is bar-pressing for food reward on a fixed ratio (FR) schedule (Ferster and Skinner, 1957) it responds so as to maintain a constant level of reinforcement earnings. That is, as the number of responses it must produce to earn a reward is increased, the number of responses the animal produces increases to compensate. If the session length is restricted, no increase in response rate occurs during runs of responses (Felton and Lyon, 1966; Killeen, 1969; Powell, 1969). If the session is long enough for the animal to earn the same number of rewards as it could when continuously reinforced, it will do so primarily by increasing the amount of time it spends working for food. An example of this is seen in a study by Collier, Hirsch and Hamlin (1972). Rats were enabled to earn food in their home

cages 24hrs. a day by lever pressing. As the fixed ratio requirement was increased from FR1 to FR20, the number of responses produced increased to maintain the number of rewards obtained at a constant level. Above FR20 responding continued to increase but not sufficiently for food earnings to be maintained at their FR1 level. Above FR160, responding reached an asymptote and food earnings declined even more steeply. However, since rats maintained their body weights to FR80, their efficiency of food utilization must have been increasing also. That this level of compensation can be increased has been shown by the same authors. They found that the degree of compensation of rats for food reward was greater if the situation allowed them to take as many food pellets as they wished at each reinforcement.

In general, fixed ratio performance for food reward is similar for to that reported for rats by Collier et al.(op. cit.). It is characterized by full compensation at low ratios, with reward rate declining thereafter (Rats: Logan, 1964l Teitelbaum, 1957; King and Gaston, 1976;Collier and Jennings, 1969. Guinea-pigs: Hirsch and Collier, 1974. Monkeys: Hamilton and Brobeck, 1964. Mice: Roper, 1975; Smart, 1970.)

Other factors affecting compensation for food reward have been identified. Lea and Roper (1977) found compensation in mice rewarded with complete diet pellets was poorer when sucrose pellets were concurrently available, and Roper (1975) found better compensation in mice when deprivation level was high and reinforcer-manipulandum distance low.

1.62 (b) Water

Water reward seems never to produce full FR compensation even at low fixed ratios. Logan (1964) egalized the amounts of work required of rats to attain their daily food and water requirements, and then compared performance for the two rewards. Unlike for food reward, compensation for water was not complete (see also Thach, 1970; Allison, 1976). Hogan and Roper (1978, p. 174-175) conclude from a review of such

studies that,

> "there is some reason to suppose that water differs intrinsically from food in the extent to which it supports behavioural compensation for increased work requirement".

1.62 (c) Heat

For heat reward, FR compensation is poor. Carlisle (1969) reports that shaved rats bar-pressing for 3sec. bursts of heat on schedules of FR1-FR20 showed sporadic responding, even at low ratios. Long post reinforcement pauses and breaks within response runs occurred, and ratio strain was also observed at the low ratio of FR15. Carlisle (1970) showed that FR performance could be improved by using chain schedules, but performance remains poorer than would be expected with food reward on a similar schedule

1.62 (d) Nest Material

For nest material as a reward, Roper (1973a) reports unusually long post reinforcement pausing and ratio strain occurred at FR15. No FR compensation occurred with a manipulandum-reinforcer distance of 6cms. When this distance is reduced as much as possible, post reinforcement pausing is shorter, ratio strain occurs later and compensation is shown to FR5 (Roper, 1975). Oley and Slotnick, (1970) report essentially similar results for rats.

1.62 (e) Aggressive Display

For aggressive display, no FR compensation has been reported. In a direct comparison of fixed ratio performance for food and aggressive display in male Bettas, Hogan, Kleist and Hutchings (1970) increased FR requirement from FR1-6. Responding remained at a constant level over ratios for display but increased to maintain reward earnings when the reinforcement was food. That FR compensation for food reward is dependant on deprivation was shown by Hogan (1978).

Bettas which were pre-fed before sessions of food reward showed no FR compensation. Those not pre-fed compensated fully. Display rewarded fish, pre-exposed to the reward stimulus (a mirror) showed similar performance to fish which were not pre-exposed. Pre-feeding food rewarded fish can therefore make their FR performance resemble that for display reward.

Grabowski and Thompson (1968) found that FR responding for display in Bettas was difficult to maintain beyond FR4 because ratio strain occurred, while Hogan et al (1970) found that ratio strain in 5 of 8 subjects had occurred by FR6. Grabowski and Thompson found that the occurrence of ratio strain could be deferred to FR24 if intermediate responses turned on coloured lights. Some compensation also occurred with double the number of responses emitted at FR1 occurring at FR24. Responding was maintained (but at a lower rate) when the lights were no longer used.

On the basis of such differences between food rewarded performance and performance for other rewards, a question recurs in the reinforcement literature. It is stated as follows: do these 'unconventional' rewards differ in their mode of action from food reward? If they do, is this difference qualitative or quantitative?

1.7 (a) The Interpretation of Reward-Related Differences In Instrumental Behaviour

Roper (1973b, 1975) found that reduction of the response reinforcer distance for mice rewarded with nest material would result in performance similar to that for food. He also found that for food reward, deprivation levels and operant-reinforcer distance interact to produce different degrees of FR compensation and susceptibility to ratio strain. He concludes that,

> "the reinforcing properties of food and paper are basically similar as regards the variables under study".

That is, when nest material does not support FR compensation

it is because it is merely a quantitatively weaker reinforcer than food.

The alternative hypothesis of a qualitative difference has been advanced by Hogan et al.(1970)and Shettleworth, (1972). Shettleworth suggests that a difference may exist between reward types which act on motivational systems,

> "...designed to maintain homeostasis by increasing effort to obtain a constant amount of some variable such as food".

and those,

> "...designed to maintain some internal state necessary for survival".
>
> Shettleworth (1972, p.13)

Hogan and Roper (1978, p.233), while admitting the temporary utility of a homeostatic/non-homeostatic distinction, consider that it is unlikely to survive experimental analysis. The major reason they advance for this is that under normal circumstances, the food intake control system does not operate in a homeostatic way, but is primarily controlled by non-regulatory factors (Collier, Hirsch and Hamlin, 1972; for water intake, Blass and Hall, 1976). This dismissal of the homeostatic/ non-homeostatic distinction, if homeostatic is taken to mean a depletion-repletion process, may be premature. Those experiments which have indicated that food intake is not controlled by deficit (e.g. Collier et al, 1972; Hirsch and Collier, 1974a; Duncan, Duncan, Hughes and Woodgush, 1970; Davies, 1977) have used animals not experimentally food deprived. When fixed ratio performance for food reward is tested in non deprived animals, or in those with little deprivation, FR compensation does not occur (e.g. mice; Roper, 1975: Betta splendens; Hogan, 1978). In studies using fixed ratio reinforcement schedules without experimental food deprivation, testing is normally for 24hrs. per day. When FR compensation does occur, animals may have undergone self-imposed deprivation before compensating for the ratio requirement. (This will be treated in more detail in ch. 13 .)

The major drawback of Shettleworth's hypothesis may not therefore lie in the distinction between homeostatic and non-homeostatic motivational systems. Instead two other important difficulties exist. The first of these, also pointed out by Hogan and Roper, concerns the identification of homeostatic systems and the biological necessity of the commodities with which they are concerned. That is, the functional concept of biological necessity has been used to answer a question of causation or mechanism. If the functional aspect of the hypothesis is removed, leaving only the suggested relation between compensation and a system that monitors and responds to the amount of a particular variable, then a testable hypothesis remains. The second major problem, and related to the previous criticism, is the assumption that all food related motivational systems are an homogenous category. That is, food is necessary, therefore it will be controlled by homeostatic factors, and it follows that all food intake systems will be similar in their modes of operation. Evidence does exist to suggest that within the category hunger motivation, species may differ in the control systems they possess.

In many omnivorous species, cellulose dilution of food material, with it's accompanying decrease in calorific value, is responded to by an increase in the quantity of food consumed. The animal therefore functions to maintain a constant rate of calorie intake (e.g. mice; Dalton, 1965: Goldfish; Rozin and Mayer, 1961: Pigs;Owens and Ridgeman, 1968). In the Guinea-pig, an herbivore, no such calorific compensation occurs (Hirsch, 1973) but body weight is kept stable by increase in the efficiency of food utilization. Cats also fail to show compensation for diet dilution, (Hirsch, 1976). A similar species difference can be seen in the response to experimental food deprivation. After food deprivation many species will increase food intake to restore body weight (e.g. gerbils: Kutscher, 1969; for other species see review by Fabry, 1969). In the Golden Hamster, however, post-fast

compensation does not occur (Silverman and Zucker, 1976). It must be concluded that despite it s obvious biological necessity, the way in which control of food intake is achieved may differ across species. For this reason, any search for a relation between the sensitivity of a system to deficit and fixed ratio compensation, must determine in advance and outside the operant situation, the nature of the control system underlying food intake.

Hogan and Roper (1978) while concluding that a homeostatic/non-homeostatic distinction would not survive experimental analysis, do suggest that differences in the properties of reinforcers are best viewed as differences in the motivational systems which underly them. The concept of a "behavioural system" which these authors adopt (p.226) leads to the view that learning is a process that changes the connections between units. These connections are seen as formed at a "central" level such that stimuli and response become associated with central co-ordinating mechanisms. They cite as an example (p.229) a rat which has learned that lever pressings and the hunger systems are associated, so that many causal factors already affecting the hunger system will now affect lever pressing. The learned behaviour so becomes a part of natural "appetitive" behaviour (sensu Craig, 1918). Thus, Hogan and Roper consider the actual connections that exist at any moment in an individual depend on it s developmental history, and it follows from this that every individual's system within a species must be unique. The possibility of species differences in motivational organisation is considered and these authors conclude that the diversity among species, and motivational systems

> "...clearly limits the kinds of generalizations that can be made about reinforcers..."
>
> p. 240

They further conclude that,

> "...given the present state of knowledge, this means empirical determination in each case, and a ragbag of post hoc explanations for any differences that might arise. The limited kinds of generalizations that can be made are, we suggest, best expressed in motivational terms".

1.7 (b) Instrumental Behaviour As An Appetitive Behaviour Suitable For Causal Analysis

Hogan and Roper's conclusions about the necessity for post-hoc explanations for the differences in instrumental performance produced by various rewards may be unduly pessimistic. Although little progress has been made in the prediction of instrumental performance characteristics from knowledge of the motivational systems underlying a particular reinforcer, it can be suggested that this is because knowledge of the functioning of those motivational systems is sparse. If operant behaviour is to be viewed as an output of a motivational system affected by that system's inputs in the same way as other appetitive behaviours, then investigations of natural appetitive behaviour can be expected to lead to predictions about instrumental performance. It follows from this suggestion that the causation of a learned behaviour may be investigated in the same way as the causation of any other behaviour. Thus, taking as an example display reward in Betta splendens, methods have been devised in the ethological tradition for investigating the causation of attack and display behaviours (see ch.3.3 for discussion). If outside the operant situation, the mechanisms involved in the causation of attack and display can be understood, then predictions can be made about the way in which these mechanisms will, in a learning situation, control the patterning of performance of the learned behaviour.

Ultimately, it would be hoped that comparative studies of reinforcers would be possible. A particular difference in the nature of the system controlling two behaviours in a species or the same behaviour in different species, would form the basis of an hypothesis about differences in the operant performance for these behaviours as rewards, or in those species for the same behaviour. However, at a preliminary stage in such a strategy, much might be learnt about the control of operant behaviour by concentrating on a single species and reward.

The Siamese fighting fish is a particularly suitable species for such an investigation, since it s aggressive display can act as a reward and methods for investigating the causation of displays are well established. In addition, unlike food intake, many easily observable changes in the behaviour of the fish occur during reinforcement. From these changes, inference may be drawn about the motivational states of the fish during reward. An attempt can then be made to relate these to the performance of the learned behaviour which follows each such reward. For these reasons, the present thesis does not directly compare instrumental performance for different reinforcers. Instead, an attempt is made to use some methods of causal analysis to investigate in some depth the functioning of the system controlling aggressive display in this species, and to relate this mode of functioning to instrumental performance for display reward.

Before doing this, a description of Betta splendens and it s display is required.

CHAPTER 2

2.1 The Experimental Subject: Betta Splendens Regan

With the exception of ch.13, all the experiments to be reported here have as their subject the domesticated form of the Siamese fighting fish (Betta splendens Regan) as described by Regan (1909).

Indigenous to Thailand (Smith, 1937, 1945) but introduced by man into other parts of Asia (e.g. Malaya; Tweedie, 1952), early workers such as Regan (1909), Weber and de Beaufort (1922) and Berg (1958) considered Betta splendens to be a species of the Anabantidae, one of the only two Anabantoid families. More recently, Liem (1963) has suggested a modified classification of the sub-order based on osteological data. He recognises four families of Anabantoidei; the Anabantidae, Belontiidae, Helostomatidae and Osphronemidae. The family Belontiidae is divided into four subfamilies with Betta splendens falling into the Macropodinae. The families and genera of the Anabantoidei and subfamilies of the Belontiidae, as represented by Liem (1963) are shown in Fig. 1 .

Three characteristics are shared by almost all the 22-25 species of Belontiidae.

1. They all possess a labarynthine organ used in breathing atmospheric air.
2. The males of most species build a bubble nest on the water surface into which the eggs are placed after spawning.
3. Fertilization of ova is achieved by means of a spawning clasp or nuptual embrace.

Before treating these characteristics in detail, some discussion is necessary of the ecological setting in which the Anabantoidei evolved.

2.2 Ecology: Climatic Cycle

The Anabantoidei are thought to have originated in tropical Asia (Darlington, 1957), and are at present distributed throughout this region, with an additional three genera

indiginous to Africa. These latter, (f. Anabantidei), considered by Liem (1963, p.43), to resemble the ancestral Anabantoid stock most closely, include the single Anabantoid genus (the South African Sandelia), which no longer inhabits a tropical or subtropical zone. With the exception of Sandelia then the description provided by Smith (1945) of climatic conditions in Thailand, home of Betta splendens, may be applicable to all Anabantoid species.

Thailand's annual climatic cycle involves a wet season of daily rainfall from April to November under the influence of the Southwest Monsoon. During this period occurs most of the average yearly precipitation which is approximately 1600mm. varying regionally from 900 to 3000mm.

This rainy season gives way to a cool dry season during the period of the Northwest Monsoon, lasting from November to February. The transition from dry to wet seasons involves a short summer.

With the onset of the wet season the streams and rivers rise, filling their beds, and becoming interconnected with marshes, pools, rice fields and irrigation canals reduced during the dry season.

As the water level rises the fish follow the flood waters into the ricefields and newly formed lakes, and by the time the water level has reached it's peak most fish have spawned.

As the flood water falls, the adults return to the rivers to be followed later by the young who become sexually mature at 3-4 months of age (Smith 1945, Forselus 1957).

2.3 Feeding

The feeding habits of the Anabantoidei within the ecological settings described cover almost all possibilities. Liem (1963, p. 53) on the basis of the identification of the various genera along with the fineness and number of gill rakers present (these are a straining mechanism, very numerous and

fine in herbiverous species barring the entry of fine food particles into the gill filaments) suggests three independant evolutionary lines, entering into three diverging adaptive zones.

The current African Anabantoids are carnivorous and these may most closely represent the ancestral Anabantoid stock. From the ancestral Anabantoids emerge three lines. The first resulting in the Osphronemids has become purely herbiverous, the second group, the Helostomatids have become specialized plankton feeders, and the third, the Belontiids, are omniverous with a trend within the family, most marked in the Trichogasterinae, towards new herbiverous zones involving much smaller foods than the Osphronemids. The evolution in two Trichogasterinae (Trichogaster and Colisa) of pairs of pelvic fin rays moveable in any direction (Steinbach, 1950) and with tastebuds on the ends (Scharrer, Smith and Palay, 1947) has accompanied this shift in feeding habits, although they may also have a role in social interactions (Picciolo, 1964).

Betta along with Trichopsis the most primitive Belontiid, may, even if omniverous, be rather closer to a carnivore than the other genera. Its carniverous nature has been attested to by Vaas, Sachlan and Wiraatmadja (1953) for Betta unimaculata on the basis of stomach content analysis (insects in the air and on the water surface), and for Betta splendens by observation of its feeding behaviour (mosquito larvae) by Smith (1937).

2.4 The Labyrinth

The periods of drought and high temperatures to which tropical freshwater fish are subject, means that the water in which they live may be for much of the year deficient in oxygen. Several unrelated fish species in South-East Asia have independently evolved apparatus which supplements the oxygen available via the gills.

All members of the catfish family, the Clariidae, inhabiting

Thailand have an accessory breathing organ on each side of the head occupying a cavity above the gills. In another family (the Heteropneustidae) the accessory breathing organs are long hollow cylinders along the muscles of each side of the vertebral column. A more primitive apparatus, a large vascularized suprabranchial cavity is found in the Ophicephalidae (Smith, 1945).

In the Anabantoidei, the labyrinth organ is derived from the epibranchial of the first gill arch and lies in the suprabranchial cavity. It is comprised of bilaterally arranged, dorsomedially oriented, pharyngeal outpocketings enclosing four bony lamellae covered with heavily vascularized epithelium. To fill the labyrinth the fish swims to the water surface and takes a mouthful of air.

The gills of Belontiidae are functional but are inadequate even in well oxygenated water without supplementary air breathing (Smith, 1945).

It is interesting to note that the only Anabantoid to move into a temperate zone, the African Sandelia, has a reduced suprabranchial cavity. (Liem, 1963, p. 64).

2.5 Nest Building

Possibly related in evolution to the breathing of atmospheric air by the Anabantoidei is the building of a bubble nest on the water surface. The fish swims to the surface takes a mouthful of air and expels it as a bubble or stream of bubbles. The durability of these are increased by a mucus secreted by the unicellular glands lining the oral cavity. The size and number of bubbles blown varies with species, with a single bubble blown after each air gulp in Betta splendens, 2-10 large bubbles being blown per mouthful of air in Macropodus opercularis, and clouds of tiny bubbles in Trichogaster leeri and T. trichopterus (Hall, 1965).

Male Betta splendens begin nest building at 3-4 months of age and nests are usually preceded by a period of some

days during which bubbles are blown apparently at random throughout the tank. After a while the male will concentrate on one particular place, usually along one tank wall or in a corner. The movements involved in nest building consist of the intake of air at the periphery of the already constructed nest (this is similar to an air gulp movement in breathing). The bubbles are then expelled under the existing nest or at its periphery. Whether or not vegetation is incorporated in the nest varies with species. Betta splendens is observed to do this occasionally.

During a bout of nest building the rate of air uptake and the following bubble placement movements are of the order of 10-20 per minute. The bouts of nest building are often interspersed by periods of parental behaviour such as "fanning" and "nest posting" (these will be described later) even though eggs or larvae are not present.

De Bruin (1977) has described a cyclical nest building pattern in isolated male Betta splendens. When a nest has been built, a male will maintain nest building behaviour for one to five days to prevent it disintegrating. These periods of nest building are interspersed with periods when no nest is present. If complete social isolation is maintained for longer than two months nest building gradually ceases, to be resumed only when a conspecific or the male's own mirror image is presented.

The factors controlling nest building are not well understood. Forselius (1957, p. 205-230) described nest buildings in Colisa lalia males (subfam. Trichogasterinae) with some data on other species, and emphasised the releasing effect of a ripe female (p. 208)

He reports that isolated Colisa males (p.350) maintained nests for several days to weeks, followed by similar periods of little or no nest building. Miller (1964) describes a similar pattern in non-isolated T. trichopterus noting that the periods without a nest were terminated if the females (continually present) came into reproductive condition. These

observations agree with those of de Bruin (1977) for Betta splendens.

Miller (1964) presents a rather different picture of the control of nest building from that of Forselius. In groups of T. trichopterus, males would build nests when females were in non-breeding condition or absent altogether, and when no eggs or young were present. Also, after spawning (which can occur without a nest), eggs and young were often left floating at the surface with only a few nest bubbles present. However, every spawning observed was eventually followed by nest building. Miller concludes that nest building, in T. trichopterus at least, may be more intimately associated with the post spawning situation than with courtship.

For Betta splendens, Braddock and Braddock (1959) conclude that there is no 'critical nest size' for spawning to occur. However, observations in this laboratory suggest that in mixed sex groups of Betta splendens, where males gradually change their behaviour towards females from overt aggression to courtship, nest building usually occurs somewhere in the middle of this transition. It may be that males who are of less than average aggressiveness or males courting larger females, who will when reproductive persist in their approaches, may occasionally succeed in spawning more rapidly than usual and thus before nest building has reached an advanced stage.

One might expect, considering the ecological circumstances of the Anabantoidei, that in part, at least, the control of nest building would involve environmental change signalling that flooding has occurred.

Observation in this laboratory, of Betta splendens nest building suggests that in addition to the releasing effects of conspecifics on nest building in isolated males (isolation being possibly a common occurrence in the wild), a sharp rise in water level or the replacing of existing tank water with fresh water is often followed by nest building in both

isolated and non-isolated males.

For Trichgaster trichopterus, Miller (1964) has suggested that the above factors may be operating and in addition reports nest building after temporarily lowering water temperature from 25° to 19° or 20°c, after raising the temperature from 20° to 25°c and after introducing a male into a well planted tank. These are the sort of environmental changes which would occur following heavy rains.

In addition, the adoption by male C. lalia of nests introduced into the tank when they have not been nest building has been described by Picciolo (1964), who notes that this stimulated territorial and nest building behaviour. Robertson and Sale (1974) describe similar nest adoptions in Betta splendens, and Braddock, Braddock and Kowalk (1960) showed that Bettas could be stimulated to nest build by presenting them with floating discs of white paper.

Several functions have been suggested for Anabantoid bubble nests. (See Wunder, 1931; Forselius, 1957 and Miller, 1964). The oxygen required by developing young would be more heavily concentrated at the water surface. As does any nest, a bubble nest serves to localize the young thus facilitating parental care and particularly defence against fish predators both conspecific (particularly the post spawning female) and non-conspecific. The effectiveness of a bubble nest as a defence against aerial predators is unknown and may rely on the camouflage of overhead or incorporated vegetation. Without some disguise or canopy it seems likely that nests would serve only to attract such predators.

The building of bubble nests by so many Anabantoids (exceptions exist, e.g. Betta anabantoides Bleeker - a mouthbreeder), may be related to their breathing of atmospheric air. The behaviour of air gulping in respiration and the intake or air for bubble making are quite similar and the very necessity for rising to the surface to breathe may militate against substrate nesting. The desertion of the

young for even brief periods could well prove disastrous. In addition to the various functions mentioned above, bubbles disperse light and may form a protective filter against bright sunlight, while disintegrating air bubbles may facilitate the development of infusoria, an important food for the fry.

As well as facilitating parental care the nest may serve to attract females. Ripe female Betta splendens introduced into a tank will often swim directly to that nest and position themselves underneath it.

2.6 Territorial Behaviour

During the non reproductive phase, (in the wild this phase occupies the dry season) Anabantoids including Betta splendens exist in relatively social groups. The size of these groups in the wild is not known but may include males and females with fairly stable hierarchical relations between individuals.

The social organisation of Colisa lalia (Forselius, 1957, p. 197) and Trichogaster trichopterus (Miller, 1964) have been described in some detail, while little is known of the behaviour of Betta splendens in permanent mixed sex groups. However, qualitative observations in this laboratory of two 20 gallon tanks heavily planted and holding respectively 5 males and 5 females, and 4 males and 3 females, accord well with the aforementioned descriptions for C. lalia and T. trichopterus. In such groups little territorial defence is seen in the non reproductive phase. Fish swim throughout the tank, remaining pale in colouration. Aggressive encounters are mainly restricted to situations in which a fish is swimming in a particular direction and another individual is "in the way". This latter fish often moves away immediately, it may then (relatively rarely) be chased at low speed for a very brief period and a nip may be directed at its caudal fin. This nip rarely lands. In Betta splendens if the obstructing fish does not immediately give way, then either the first individual will do so, or it

will exhibit a frontal display, erecting its gill covers. If the receiver of the display still does not give way then the first individual will turn broadside and erect its medial fins. If the receiver flees at this stage it seems more likely to be chased and nipped than if it had fled immediately. The second individual, male or female, may itself return the display but in the non reproductive phase few encounters involve more than a single occurrence of frontal and lateral display in each fish.

In accord with Miller's (1964) description for T. trichopterus, where clear differences in the sizes of the fish are evident, the smaller is almost always subordinate, with the exception of males which are only slightly smaller than females. Between individuals a fairly stable dominance hierarchy is evident, and the introduction of a new male into an established group will eventually result in his fighting all members of the group until his position in the hierarchy is established. In this situation in Betta splendens, three way fights may occur, and almost all prolonged agonistic behaviour between a pair results in an outbreak of chasing, nipping and display among nearby fish.

After a period in such a non reproductive state, either spontaneously or after the environmental changes described earlier, a particular male may begin to darken in colour and localize its locomotion, rapidly approaching and displaying to any other individual in a particular tank area. Attacks also become markedly more vigourous. After displacing another fish the male may chase it briefly, but will return to its original position in the tank. This territorial behaviour may last for some days with the resident attacking both male and female intruders before a nest is constructed and females are courted.

If two males are establishing territories in the same tank, then more prolonged fights may occur. These fights are in general still shorter in duration than fights between unfamiliar males or males isolated between tests. This latter

situation is the one most often used in the experimental investigations of aggressive behaviour in Betta splendens (e.g. Simpson, 1968; Dore, le Febvre and Ducharme, 1978; Baenninger, Bergman and Baenninger, 1969) and in operant experiments using display reward (e.g. Hogan, Kleist and Hutchings, 1970; and the present thesis). The course of such a fight is described in a later section.

It seems likely that in group maintained Bettas, which shift periodically from non-reproductive to territorial phases and hence from relatively non-agressive to aggressive states, that some of the effects of hierarchy established during the non-reproductive phase remain and influence the outcome of territorial encounters. It has been suggested by Greenberg (1947) in connection with territory and social hierarchy in the green sunfish (Lepomis cyanellus), that,

> "...the principles of hierarchy and territory are not sharply separate..."

and that,

> "It is highly probable that hierarchical relations of some sort exist in every instance of territory..."

No data is available on the density of Betta splendens in the wild nor on the average size of territories, but in the laboratory situations the number and size of territories established in a tank of given dimensions is dependant on the density of vegetation with dense cover resulting in a larger number of smaller territories. Other factors involved are the relative and absolute sizes of males and their positions in the reproductive cycle.

2.7 Sexual And Parental Behaviour

The sexual and parental behaviour of Betta splendens has been described by Forselius (1957), Rainwater and Miller (1966) and Kuhme (1961). The optimal conditions for its occurrence have been described by Goodrich and Taylor (1934).

Simpson (1968, p. 2) notes that all the movements

occurring in Betta splendens threat display also occur in its courtship. The early stages of a sexual interaction are always characterized by threat behaviour. The male swims about close to the nest and on seeing a female, approaches her with his gill covers (opercula) erect. Before or during this approach, the male's colour darkens considerably. On coming within a fish length of the female, the male turns his body broadside, so that he is at a 90° angle to her. The female will, if she is receptive, also darken in pigmentation, show 4 dark vertical bands on her flank, and have a gold coloured ventral surface. This surface (showing clearly an egg papilla) is then presented to the male, who swims away from the female towards the nest. This leading is accompanied by undulating movements of the body and is punctuated by halts during which the medial fins are erected. This is followed by a return to the female with similar swimming movements, and further withdrawals (for the comparable "zig-zag" movement of the 3-spined stickleback, see van Iersel, 1953). The periods during which the male is close to the female, may vary in duration and include a series of alternations between facing with gill-covers erect (frontal display) and broadside orientation with the medial fins erect. Biting and ramming may occur immediately following approaches (usually the more rapid approaches) and the female may be chased. If the female does not follow the male to the nest quickly enough, or if she follows too quickly, the male will increase his attacks. These may be followed by the female adopting a submissive posture in which the body pales in colouration, the fins are slack and 3 horizontal bands appear on the flank. The long body axis is also held oblique to the water surface.

If the female is tolerated under the nest, because the male's aggressiveness has been sufficiently reduced, pseudo-copulation occurs. The male clasps the upside-down female and makes spasmodic body movements. This is followed by the male and female remaining motionless. The female releases eggs which sink to the substrate while the male presumably ejects sperm. Both male and female then sink to the bottom

(swimming inhibition) from which the male is first to recover. He collects the eggs in his mouth, swims up to the nest and spits them into it. The female follows suit. The number of eggs released in the series of 10-15 such spawnings that occur over a 2-3hr. period may be as high as 100. After egg collection, the female is chased away from the nest. If she is not chased away she will begin to eat the eggs.

Care of the young is entirely the province of the male . After the female has been driven off, he begins to nest-build again, placing air bubbles underneath the eggs so that they are completely enveloped in the nest. This behaviour is interspersed with periods of fanning in which the male is oriented towards the surface with upward beatings of the pectoral fins and undulating movements of the body, thus driving a stream of water past the eggs to provide rich oxygen supply. Such periods under the nest sometimes include the fish remaining motionless in an oblique posture with the medial fins partly erected (nest posting).

After 2-3 days the eggs hatch and the young leave the nest. The male responds by swimming about under the nest collecting them in his mouth. They will then be spat into the nest. This behaviour lasts for 5-7 days after hatching, after which time the young can no longer feed from their embryo sacs. The behaviour of collecting the young then disappears. The nest may then be allowed to disintegrate.

2.8 Aggressive Behaviour

Full descriptions of Betta splendens threat display have been provided by Lissman (1932) Forselius (1957) and Simpson (1968). The initial response of a male to another male is identical to that shown to a female. The resident male darkens in colour and advances towards the intruder with its gill covers erect (frontal display). The intruder will usually respond to this by turning broadside with erect

medial fins (lateral display). After a few seconds, the male in lateral display will turn to face its rival with a frontal display. This will be responded to by a lateral display in the second fish. The fight continues with alternations between frontal and lateral display, with both fish rarely being in similar postures for long. During lateral display, tail beating and the gulping of air occur. Biting may follow frontal or lateral display. A behaviour which occurs only several minutes into the fight and often terminates it is jaw-locking. The opponents turn to face at the same moment with open jaws, which they interlock. Often after prolonged twisting about their long body axes, they will sink to the substrate still locked together. While jaw-locking neither fish can rise to the surface to air gulp and this behaviour may result in one fish having to submit first. If no submission occurs the fish will disengage and air gulp simultaneously before engaging in further display. Fights are terminated abruptly when one of the fish ceases to display, pales in colouration and shows 3 horizontal bands on the flank. It then retreats slowly, usually maintaining ~~this posture~~ a broadside orientation until it eventually breaks into rapid flight.

Figure 1

The families, subfamilies and genera of the suborder Anabantoidei (after Liem, 1963).

Suborder Anabantoidei

Family	Subfamily	Genera
Anabantidae		Anabas, Ctenopoma, Sandelia.
Helostomatidae		Helostoma.
Osphronemidae		Osphronemus.
Belontiidae	Belontiinae	Belontia.
	Macropodinae	Betta, Trichopsis, Macropodus, Parosphronemus, Malpulutta.
	Trichogasterinae	Sphearichthys, Parasphaerichthys, Colisa, Trichogaster.

CHAPTER 3

3.1 (a) The Causation of Betta Splendens Aggressive Display

If an attempt is to be made to relate the changes in display reward and the performance characteristics of the operant behaviour, the nature of the systems underlying display must be considered.

The simplest such system would be one in which a single "aggressiveness" variable was responsible for all display components. These components might simply occur at different thresholds of this single variable. However, recent experiments suggest that a more complex system may underly display in Betta splendens. In the instrumental situation results have been reported which appear to indicate that two motivational states are involved in aggressive display. The existence of these two causal factors, aggression and fear, has been inferred from the behaviour of Bettas during display reward, and it has been suggested that they are also involved in the control of instrumental performance for display reward.

3.1 (b) The Role of Fear

In comparing the T-maze performance of male Betta splendens for reinforcement with displaying and non-displaying male conspecifics, Bols (1977), found a higher level of performance for displaying stimuli. She also describes several differences in the aggressive display elicited during reinforcement by these stimuli.

Bols' observations were a good deal more detailed than is usual for this area of study, and suggested that the instrumental performance differences observed were not merely quantative. That is displaying stimulus males did not simply produce higher levels of aggressiveness and consequently higher levels of performance than non-displaying males. Instead, Bols suggests that differing strengths of two intervening variables, aggressiveness and fear may be involved in producing the difference in reinforcing effectiveness observed. This conclusion is based on the observation that "escape" behaviours were elicited by non-displaying males.

These behaviours included "thrashing" described as,

> "vigorous undulations of the body performed while moving up and down against the transparent wall of the goal box".

Thrashing never occurred against the wall adjacent to the stimulus fish. Also observed were high levels of immobility and "turning back" in the runway. Other behaviour to the non-displaying stimulus, Bols attributes to conflict, e.g.

> "...swimming rapidly towards, then away from, the goal-box, while assuming the dark colouration characteristic of aggressive arousal and displaying sporadically".

Bols suggests that fearful behaviour to a subordinate may occur because the subordinate does not behave in response to the subjects display in a way that confirms the subject's expectancies (after Bastock, Morris and Moynihan, 1953 and McFarland, 1966).

Retreating by male Bettas from an aggression eliciting stimulus has also been described by Simpson (1968, p. 10, for conspecifics; p. 46 for mirror; p. 47 for model male) and by de Bruin (1977) for mirror elicited display. This latter author considers withdrawals to be an initial stage in aggressive display and classifies males on the basis of the amounts of withdrawal they show.

Lateral display in Betta splendens may also be attributable to the action of fear. This component of Betta's aggressive display has probable homologues in several species. Barlow, (1962) discussed the possible function and causation of this display in Badis badis and considered it dependent on conflict between flight and aggressive motivations. This is a similar conclusion to that reached for Anabantids by Forselius (1957, p. 431). The primary source of evidence for this interpretation is that this display often precedes or follows overt aggression or flight. However, this conclusion differs from that of Baerends (1957) who suggested that erection of the medial fins is most dependent on attack.

That lateral display may not depend on specific motivational

systems is suggested by Myrberg (1965, p. 314) who showed that for cichlids, lateral display precedes "explosive swimming" and may be more closely related to locomotory co-ordination than to specific motivational systems. That the pelvic fins act as horizontal rudders was shown by Breder (1924) and the role of medial fin erection in the prevention of "yawing" (side to side motion) and "rolling" has been shown by Gray (1953). Baerends and Baerends van Roon (1950) discuss the contexts in which such behaviours may have no signal functions.

Some authors have found no evidence for fear in the causation of Betta displays. Using factor analysis, Robertson and Sale (1974) investigated male Betta splendens' aggressive behaviour. They conclude that there are three primary influences on the display shown. The first and most important is an influence to perform all display components. The second is to perform specific activities such as raised opercula, while the third is responsible for approaching and biting. An important result of this study is that none of the influences identified approximate to a fear dimension, while a single "aggressiveness" variable would not be sufficient to account for even a single display component and overt attack together.

Initially, Simpson (1968, p. 22) hypothesised that a parallel might exist between fighting in the 3-spined sticklback (Gasterosteus aculeatus) and display in Betta splendens, with facing (frontal display) in Betta being the equivalent of chasing in the sticklback and the broadside orientation (lateral display) of Betta being equivalent to stickleback fleeing. However, after finding that most of the measures of Betta display used are correlated, he concludes that the

> "...failure to find an independent fear of fleeing 'dimension' among the display measures suggests that such an hypothesis is unnecessarily complicated for Betta display".

Bols (1977) observed that the retreating was elicited in Bettas by subordinates and the explanation of this in

terms of expectancy has been mentioned. A possible mechanism for the elicitation of fear by a submissive male does therefore exist, but the plausability of such behaviour occurring at all must be questioned on functional grounds. It is difficult to see why a non-displaying male should elicit more overt escape than does a male who displays and who therefore is a rival for such resources as territory and females. There is of course some danger here of introducing functional criteria into causal analysis against which Baerends (1971, p. 300) has strongly warned. However, the aim here is not to reject a priori the fear hypothesis of the causation of behaviour to a subordinate, but to suggest that further analysis of subordinate elicited behaviour in terms of its causation, along with consideration of its function may be useful.

To properly evaluate Bols' "fear" interpretation of subordinate elicited behaviour, it is first necessary to consider the methods by which causal analysis may be carried out and some current views of the causation of displays.

3.2 Methods For The Causal Analysis of Displays

Tinbergen (1959, p. 50; 1964) outlined 3 major methods for inferring the causal basis of a display. These and additional sources critically reviewed by Hinde (1970, p. 30) will be briefly described.

1. Situation evidence may provide clues about causation. If, for example, threat display occurs most often on the boundaries of a territory, then it may involve conflicting tendencies to attack and escape from the eliciting stimulus.
2. Comparison of the morphology of a display behaviour with other behaviours of presumably known causation may indicate that it is similarly caused. A male may turn to face its rival with a motor pattern resembling an attack movement. This turning to face may be caused primarily by attack tendencies.
3. Behaviour may accompany the display which indicates by its form the causal factors predominating in the control

of that display. So if a displaying male Betta moves away from its opponent, the display may involve the predomination of flight tendencies (e.g. Bols, 1977 for Betta splendens).

4. The sequential and temporal correlations between display components and overt attack or fleeing movements may indicate the degree to which each component is controlled by attack or flight tendencies (for example. see Moynihan, 1955; Stokes, 1962; Kruijt, 1964; Blurton-Jones, 1968). The method of sequential correlations has certain associated problems.

a) Changes in the behaviour of the displaying animal, are often consequences of changes in the behaviour eliciting stimulus. This may require the use of models for stimulus control, but the possibility that unresponsiveness may itself determine behaviour cannot be ruled out.

b) Many displays are seldom followed by "pure" expressions of the tendency of interest. The same display may be followed sometimes by attack, sometimes by flight and sometimes by staying put.

c) Movements may be associated in time because they are low priority behaviours which occur only when higher priority tendencies are absent or have inhibited each other.

The method of temporal correlations also involves some difficulties.

a) Because this method correlates the amounts of the various behaviours occurring during a chosen time interval, the results are dependent on the length of that interval.

b) It provides less information about the organisation of the behaviour than does sequential correlation. The following example is given by Hinde (1970, p. 372):

> If A follows B as often as B follows A these behaviours are likely to share causal factors. However, if B follows A, but A does not follow B, A may be causal with respect to B.

This information is lost in temporal analysis. One advantage of the temporal method of correlation is that it can relate different measures of behaviour, expressing for example, relations between their frequencies and durations. An extension of the methods of sequential and temporal correlations is the subsequent application of factor analysis (for examples, see Wiepkema, 1961; Robertson and Sale, 1974).

5. Manipulation of the tendencies postulated as underlying a display is a more direct means of establishing the causation of that display. Blurton-Jones (1958/59) found that display in a pair of tame Canada geese (Branta canadesis) could be produced by the simultaneous presentation of two stimuli, which alone produced attack and flight respectively. This provides strong evidence of the dual causation of the displays. This method was also used systematically in investigating threat displays in the Great tit (Parus major) by Blurton-Jones (1968). A rather different kind of manipulation, but one based on similar logic, was used by Wiepkema (1961, p. 158) in a study of the possible aggressive tendencies underlying behaviours occurring in a courtship context in the male bitterling (Rhodeus amarus). Before presentation of a female, males were shown a large male which elicited fleeing, or a small male which elicited chasing. The internal states induced by these threat pretreatments, fear and aggressive tendencies respectively, persisted into the courtship test and the effects of their strengths on sexual behaviour could be evaluated. By this means it was found that two courtship behaviours, ejaculation and quivering, were reduced by increases in aggression, while another sexual movement, skimming, was unaffected. Manipulations of the supposed tendency underlying a display need not be direct. The pivoting behaviour of Goldfinches increases in frequency as the breeding season progresses. This naturally induced change in the behaviour is one source of evidence for its sexual causation (Hinde, 1955/1956).

It must be emphasised that all the methods outlined have their own particular limitations. Because of this, Hinde (1970, p. 372) points out that.

> "...the understanding of any display demands the use of at least several of the lines of evidence discussed here..."

The method used by Bols (1977) to identify the causal factors underlying reward elicited behaviour in her T-maze experiment is a variant of method 2 outlined above. Because the behaviour involves locomotion away from the conspecific, it is concluded that fear is the cause. It can be suggested that not only is this method one of the weakest of those described, but that its use alone provides insufficient evidence for identifying the causation of a behaviour.

In discussing Bols' experiments Hogan and Roper(1978) cite Tinbergen's (1952) view that displays reflect the action of more than one motivational system. They imply that since conflict between motivational systems has been implicated in the causation of some displays in some species (the conflict hypothesis), it is to be expected in Betta threat display. In attempting to relate reward elicited displays and instrumental behaviour, it is necessary to consider current views of the causation of displays and in particular the status of the conflict hypothesis. The following discussions will outline the current state of knowledge about the evolution and causation of displays, and will try to evaluate the degree to which these concepts would be useful in investigation of reward elicited display behaviour.

3.3 The Causation of Displays and the Conflict Hypothesis

A full discussion of the evolution and present causation of displays will not be attempted here. The present discussion will restrict itself to a summary of some of the most influential views proposed and consider their implications for the present investigations of Betta threat display.

Three main sources of displays have been recognised

(Tinbergen 1952, see Hinde, 1970 for review).

1. Intention movements: incomplete or preparatory movements whose causation is identifiable because they resemble in form a causally unambiguous activity, e.g. rythmic wingflapping in the cormorant as intention fleeing (Kortlandt, 1940) the "upright" posture of the herring gull (Tinbergen, 1959).
2. Derived activities: if two behaviour patterns are morphologically similar but occur in different functional contexts, the phylogenetically oldest context is considered the one from which the display is derived.
3. Autonomic response such as skin colour changes may become part of a display.

The conflict hypothesis about the evolution of displays attempts to account for the way in which the above precursors become integrated in the complex behaviour pattern which is display. It is to a considerable extent an hypothesis about the nature of ancestral motivational systems and about their interaction. When conflicting drives or tendencies are simultaneously aroused (e.g. fear and aggression) the intention movements of the overt behaviours controlled by these drives (in this case flight and attack) occur. Threat displays therefore arose from the interaction of attack and escape drives, while courtship arose from one or both of these and the sex drive.

Although developed to account for the evolution of displays, the conflict hypothesis has been used to account for the current causation of displays, (e.g. Moynihan, 1958 for threat in Larus delawerensis). The question of whether it is appropriate to adopt this hypothesis and apply it to the problem of aggressive display and display reward in Betta splendens depends to a great extent on the degree to which it is currently accepted. It will be argued here, that it is subject to so much questioning at present that it may not be useful to describe displays in conflict terms in the context of the present research. Views of the nature of

those causal factors which come into conflict to cause displays have changed considerably since the conflict hypothesis was first advanced. Since the critiques of unitary drive conceptions of motivation presented by Hinde (1956, 1959) the assumtion that all functionally related behaviours are similarly caused is untenable. Neither can it be assumed that behaviour sequences are necessarily terminated by the activity an observer considers its functional end point (e.g. ejaculation does not lower sexual tendencies in male bitterlings: Wiepkema, 1961). The concept of the consummatory response has therefore changed.

In addition, the entities which are supposed to come into conflict may not always be major causal factors; indeed the usefulness of such factors has been questioned. Instead it has been suggested that conflict formulations be replaced by incompatibilities between specific responses (Andrew, 1972).

The ritualization of displays in evolution can include their emancipation from the causal factors which once controlled them. The shifting of the control of a behaviour from one motivational system to another (e.g. food begging in gull courtship) and the development of "typical intensity" (Morris, 1957) mean that even a behaviour pattern whose causation seems obvious because of its form (e.g. an advance-retreat pattern in an aggressive display) can be controlled by factors different from those controlling it early in its evolution as a display. Indeed, theoretical considerations have led to the questioning of whether threat displays do in fact reflect the underlying state of attack readiness (aggressiveness) of the actor (Caryl, 1979).

Because of these considerations the studies reported in this thesis will make no assumptions about the role of conflict in Betta threat display. Furthermore, it will not be assumed that all aggressive display components are caused by a simple aggressiveness factor, but instead each component and different measures of the same component will be treated separately

until evidence suggests they share causation.

Causal tendencies will be conceived of in terms similar to those used by Heiligenberg (1974), that is, the animals' "behavioural state of readiness" (tendency) will be measured by its "rate" of performance of the behaviour. Although "tendency", as it will be used in some of the investigations reported , will have drive-like implications, such usage will only be assumed useful at the gross level of analysis of a behaviour pattern. Furthermore, experiments will attempt primarily to describe in empirical terms the relations between displays and each other, and displays and other behaviours including instrumental behaviour. The results reported should then retain their usefulness independent of the way in which these relations are interpreted in motivational terms.

CHAPTER 4

4.1 General Methods

The methods described here apply to all the experiments with Betta splendens reported in this thesis. When deviations from these occur, they will be described in the relevant sections.

4.1 (a) Subjects and Initial Maintenance

Adult male domesticated Betta splendens were obtained from a local supplier and maintained individually in perspex tanks kept in an aquarium room. Fish were 3-5cms. long (excluding caudal fin). Visual isolation was accomplished by sliding large pieces of white card between adjacent tanks. The colour of fish varied, but was mainly a blue/green/red mixture. Pale coloured fish (e.g. yellow or white) were never used. Perspex tanks measuring 22.5x35x21cms. contained gravel to a depth of 2cms. and aged preheated tap water to a depth of 14cms. This depth was maintained by adding aged preheated water every three days if necessary. Tank water was maintained at $27^{\circ} \pm 1^{\circ}C$ by means of general room heating. Feeding is with proprietary dried fish food supplemented occasionally with dried or live tubifex. Food was administered twice daily, (11a.m. and 7p.m.). A 12hr. day/night cycle was maintained (9a.m. - 9p.m.) manually.

All fish were maintained under these conditions for at least two weeks and until they had constructed at least one nest before being used in any experiment. These conditions apply for both experimental subjects and stimulus fish.

4.1 (b) Apparatus

The testing apparatus forms the basis of the operant situation to be described later (ch. 6), and is illustrated in Fig. 2. It consists of a sound damping cubicle 84x84x100cms. open on one side for observations to be made. Built into this cubicle was a plexiglass chamber 26x27x40cms. with an open front and and a hinged transparent lid 31x18cms. with a 10x10cms.

section cut away. The three side walls of this chamber were covered on the inside with white card. The subject's home tank complete with its heater-thermostat unit could be slotted into the chamber via its open front wall. Illumination of the chamber was by general room illumination and in addition a 150watt lamp was suspended from the cubicle roof. The distance from the lamp to the tank water surface was 50cms. In front of the sound damping cubicle was a table, behind which the observer was seated. The distance from observer to the subject's tank was approximately .8m.

The presentation of stimulus fish was accomplished by placing the fish in a transparent cylindrical glass container, 14cms. high and 6.5cms. in diameter, the top of which was open. This stimulus container was filled with gravel to a depth of 2cms. and its base masked with black tape, a vertical distance of 2cms. This container was placed in the subject's home tank by lowering it through the test chamber roof cut-away.

To control the duration of stimulus presentation, a cylinder of thin plastic open at both ends was used to cover the stimulus container. Its dimensions of 18x7.5cms. allow it to fit over the stimulus container, masking it and preventing visual contact between subject and stimulus. This cylindrical cover could be raised and lowered by means of a cord attached to one of its open ends by means of a bent piece of "Meccano" (see Fig. 2). The cord from the top of the cover ran vertically to the cubicle ceiling, passed through a ring mounted there and down to a circular aperture in the back wall of the cubicle. This aperture also had a guiding ring through which the cord passed and ran across the experimental room a distance of 2ms. to a motor driven pulley wheel 12cms. in diameter. The activation of the motor in a forward direction rotated the pulley wheel which via the cord lifted the cover a distance of 13cms.. The motor automatically stopped after this distance due to the action of a cut-out microswitch thrown by a bar protruding from the pulley wheel. The position of the microswitch was adjustable. A similar microswitch

determined the angular distance travelled by the pulley in the opposite direction, when lowering the cover to terminate a presentation.

Two switches situated on the table in front of the experimenter allowed the motor to be driven in the two directions, one raising the cover and one to lower it. A third switch allowed the experimenter to illuminate the chamber lamp.

The stimulus container cover could be fitted over the container before it was placed in the subject's tank. Visual contact between fish could not therefore occur until the motor was activated and the cover raised.

Observations were recorded by means of a W.R.A.T.S. computer compatible event recording system (White, 1971).* This consists of a 39 key keyboard which inputs to a Uher portable tape recorder. The magnetic tape was played back into the departmental LINC-8 computer transcribing the data onto punched paper tape. These tapes were later analyzed on the Edinburgh Regional Computing Centre's ICL 4-75 computer. The keyboard and tape recorder were situated on the table between experimenter and experimental chamber. Experimental sessions were timed with a Smith's mechanical timer.

4.1 (c) Maintenance During Experiments

On being selected for an experiment fish were transferred in their home tanks to a room nearer that in which experiments are conducted (the pre-experimental room). This was to reduce the distance fish must be moved for testing. The 12hr. diurnal cycle of previous maintenance conditions was maintained here unchanged but automatically controlled. Water temperature was kept at 27°C by providing each tank with a heater-thermostat

*Modified by D. Wight of the department's electronics laboratory.

unit. Feeding and maintenance of tank water levels were carried out as before. Fish were maintained under these conditions for at least one day before being used in an experiment.

Initial maintenance in the aquarium and maintenance during experiments was as described for all the experiments with Betta splendens reported in this thesis.

4.1 (d) Procedures Preliminary To Testing:

The subject was fed in its home tank in the pre-experimental room. This feeding was in addition to the twice daily feed described in 4.1 (a). Ten minutes later its heater thermostat unit was disconnected and the subject was carried in its home tank a distance of 8-10m. to the experimental room. The tank was then inserted into the test chamber (as in Fig. 1) and the heater thermostat was reconnected. Illumination was at this point by means of general room lighting (strip lights). The fish was here left undisturbed for 10mins.

The stimulus fish assigned to that subject for the test session was caught by dip net, removed from its home tank and placed in the stimulus container described in 4.1 (b). This container had previously been washed thoroughly, filled with water from the home tank of that stimulus fish, and contained a 2cm. layer of gravel. The volume of water in the stimulus container was such that its surface was level with the water surface in subject's tank when it was placed inside. The container with its stimulus fish was then placed on a table and a small amount of food was presented. The fish was then left undisturbed for 5mins. before being carried to the experimental room.

4.2 Behaviours Recorded

The behaviour categories described below were derived from pilot studies and apply only to the subject fish. The

behaviour of stimulus fish was always observed simultaneously, using both some categories used for subjects along with others. Data from stimulus fish were not, however, used in this thesis.

Some of the behaviours identified for subjects can be described in terms of both their frequency and duration. When both of these were measured, they will be referred to as separate "behaviours". The display components identified and recorded for subjects were as follows:

Approach (Ap): When the subject was moved to a position near the stimulus container such that its pelvic fins were within one fish length of it, the approach key was depressed. This behaviour was recorded in terms of its frequency only.

Withdrawal (Wi): When the subject swam away from the stimulus container such that its pelvic fins were further than one fish length away from it, a withdrawal was recorded (frequency only).

Gill Cover Erection (GCE): When the gill covers were erected when the subject was further from the stimulus container than one fish length GCE was recorded (both frequency and duration).

Frontal Display (FD): The subject faced the stimulus fish with partially or fully lowered medial fins and erected its gill covers. FD was recorded only when the subject was within one fish length of the stimulus container. The behaviour is comparable to the "challenge" of Braddock and Braddock (1955) and the "frontal display" of de Bruin (1977). Both frequency and duration were recorded.

Lateral Display (LD): The subject turned broadside to the stimulus fish within one fish length of the stimulus container. Simultaneously the gill covers were lowered (if it followed FD), the medial fins fully erected and the caudal fin partially or fully spread. LD is comparable to the "parallelstellung" of Lissman (1933), the "agressive display" of Peeke and Peeke (1970), and the "lateral display" of de Bruin (1977). Both

frequency and duration were recorded.

Air Gulping (AG): This behaviour was recorded when the subject swam to the surface, took a mouthful of air and dropped below the surface again. This behaviour could occur both near and away from the stimulus container but only when it occurred near was it maintained for several seconds along with lateral display. This latter form of AG has been termed opercular aeration by de Bruin (1977) and has also been described by Dore, le Febvre and Ducharme (1978). While in lateral display the fish holds its mouth at the water surface and repeatedly gulps air. This is accompanied by or followed by the extrusion of large air bubbles from behind the gill covers or from the mouth. Air gulping away from the stimulus fish and as it occurs close to it, are often morphologically quite distinct. However, the single short air gulp does occur close to the stimulus and usually while the fish is in lateral display. This lateral display may diminish in intensity somewhat but may not terminate entirely. The difficulty for the observer then is to decide when the fish rising to the surface from a display is going to perform a brief air gulping movement or an extended opercular aeration maintaining lateral display. For this reason the present series of experiments did not distinguish between air gulping and opercular aeration. Instead, the AG key was depressed for as long as the air gulps persisted. This resulted in momentary key depressions for normal air gulps and protracted ones for opercular aeration. The total durations of AG during sessions did, because single air gulps were very short, reflect primarily opercular aeration. Also for this reason, the LD key was not depressed during air gulps, instead the duration of AG will be considered to reflect the duration of air gulping with medial fins erect. In encounters between male Bettas, it seems that air gulping and opercular aeration are in fact on a continuum such that as the fight progresses air gulp duration increases and AG becomes opercular aeration. In later experiments no confounding of air gulps with and without medial fins erect occurred

because stimulus presentations were responded to solely by staying near the stimulus and AG there always occurred with some degree of medial fin erection.

Tail Beating (TB): While in lateral display or during protracted air gulps, a fish would repeatedly beat its cupped caudal fin, thus directing a jet of water at the opponent. Simpson (1968) notes that the rapidity and vigour of this movement distinguishes it from the sinuous undulations observed to accompany lateral display (Thomson and Sturm 1965a, 1965b). Since Dykgraaf (1933) showed that the lateral line organ is sensitive to mechanical stimuli, such as water currents, tail beats may indicate the strength of the actor.

Biting (Bi): A vigorous lunge at the stimulus container in which open mouthed contact was made and the actor "rebounded" to some degree after contact. This behaviour was always performed with the gill covers lowered. Only the frequency of Bi was recorded.

Butting (Bu): The fish faced the stimulus, often with gill covers erect, and repeatedly made contact with the stimulus container. The lowering of the gill covers was often quite gradual and mouth to container contact was almost continuous as the fish swam in a direction directly "into" the stimulus container. This swimming movement often took the fish around the container, traversing its surface with the mouth. This behaviour is comparable to the "nips" of Simpson (1968) and the "thrusting" of Forselius (1957). De Bruin (1977) includes in "butting" only those movements in which the mouth remains open but this practice was not followed here. In practice biting and butting were easily distinguishable mainly because bites involved perceptible (they were often heard) rebounds from the stimulus container. Butting was recorded in terms of both frequency and duration.

Undulating Swimming (Usw): Recorded only when the subject was greater than one fish length from the stimulus container,

this behaviour is a forward swimming movement in which the body moves sinuously. The medial fins are held partially or fully erect. The behaviour recorded included both the "zig-zags" and "vivid swimming" described by Simpson (1968).

Stop With Medial Fins Erect (StME): Periods of swimming away from and towards the stimulus fish were often punctuated by this behaviour. The fish stops, lowering its pelvic fins and partly or fully erecting its medial fins. This behaviour was usually, but not always performed broadside on to the stimulus fish. With the exception of the pelvic fin position and its performance at a greater distance from the stimulus this behaviour is quite similar to lateral display. Both undulating swimming and stops with medial fins erect have been described as occurring to both male and female stimuli, Simpson (1968). Forselius (1957) suggests that the number of stops while approaching and withdrawing from a female may indicate the level of aggression in the male. In inter-male encounters de Bruin (1977) and Baenninger et al. (1969) note that the intensity of these behaviours is somewhat less than to a female. Both frequency and duration were recorded.

Wall Swimming (Wls): Described by Bols (1977) as "thrashing", the male swims vigorously along the tank wall often with partly erected medial fins and usually changing direction several times during a bout. Gill cover erection never occurred during this behaviour and for this reason it is not likely that it was a response to the fish's own reflection in the tank wall. To distinguish it from undulating swimming which often occurred close to the tank wall, wall swimming was only recorded when the fish's head was oriented to some degree towards the tank wall. Both frequency and duration were recorded.

Nest Building (NB): The male rises to the surface taking air into its mouth and expelling it as a bubble or series of bubbles. If a nest is already part constructed air is taken at the periphery and released at the edge of the nest or underneath it. The position adopted by the male allowed

easy identification of this behaviour since the fish's body length was almost verically inclined. This behaviour occurred in fairly discrete bouts so both bout frequency and duration were recorded.

Fanning (Fan): The male positioned itself under the nest, head upwards, beating its pectoral fins "backwards". i.e. directing water up towards the nest, and maintaining itself stationary by movements of the caudal fin. Laudien (1965) terms this behaviour "pendeln". Both frequency and duration were recorded.

Nest Posting (NP): This behaviour was recorded when the male was positioned motionless under the nest with head upwards and fins slack (frequency and duration).

4.3 Statistical Methods

The behavioural measures used in these experiments were for the most part not normally distributed, homogeneity of variance was also rare. For these reasons, and the small numbers of subjects used in the majority of experiments the statistical tests used were, with only a few exceptions, nonparametric. Significant levels are in general reported in the relevant text while detailed results of testing, e.g. size of chi^2, are shown with the relevant figure or table. Tests used are referred to in the text by their standard abbreviated names. Full names are given in the relevant figures and tables. Unless otherwise stated statistical tests used are described by Siegel (1956).

Since the completion of this thesis, Page's non-parametric test for monotonic trend* was brought to my attention. Wherever Friedman's 2-way analysis of variance is used but the hypothesis implies a monotonic trend, Page's L will be reported.

* Page, E.B., (1963) Ordered hypotheses for multiple treatments: a significance test for linear ranks. J. Am. Stat. Assn. 3, 216-230.

Figure 2

A: The testing and behaviour recording apparatus.

B: The position of the stimulus container in the subject's home tank.

a - Sound damping cubicle

b - Stimulus cover

c - Test chamber

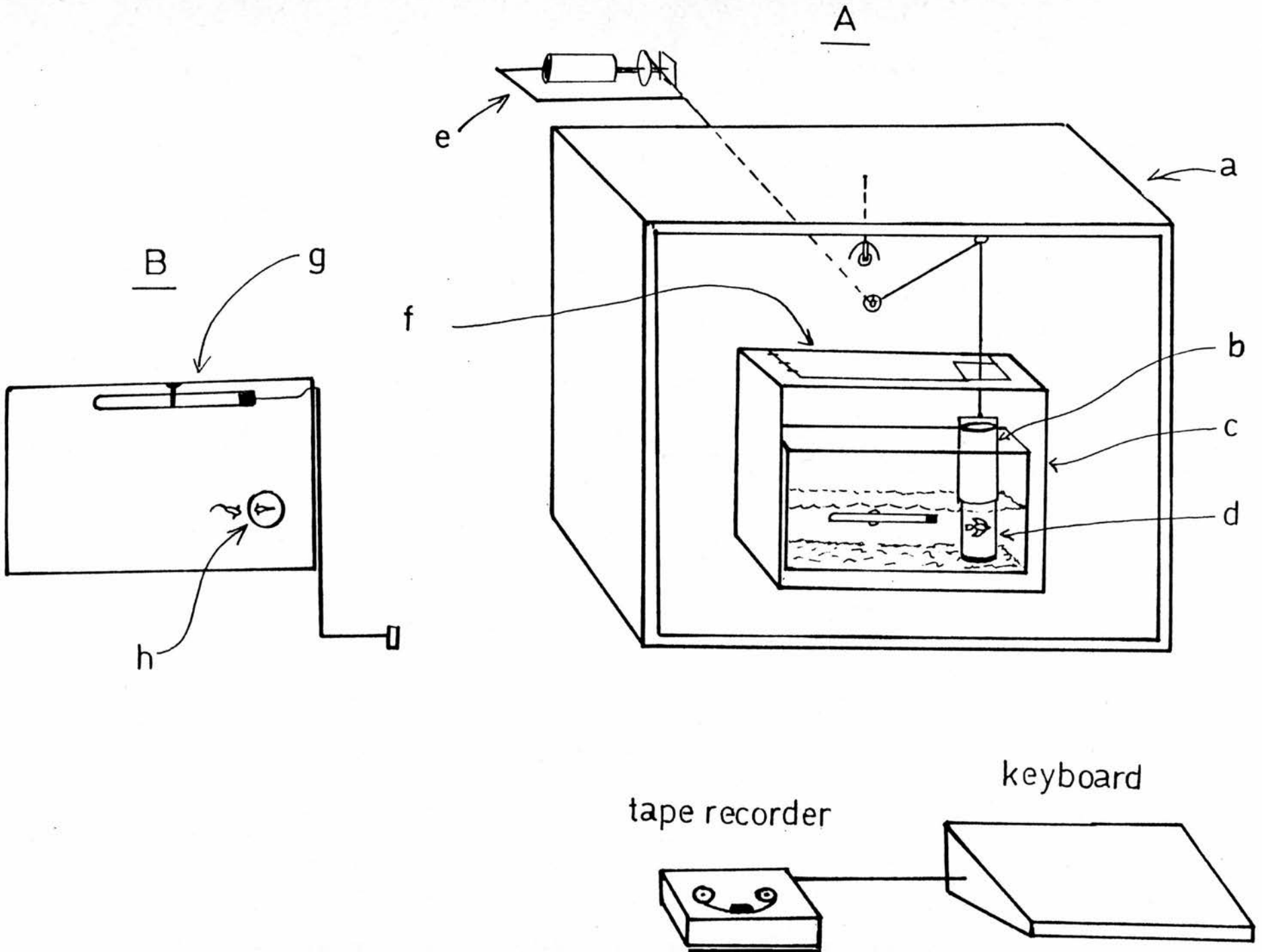
d - Stimulus container

e - Motor and pulley

f - Test chamber

g - Heater thermostat

h - Stimulus container


A
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tape recorder

CHAPTER 5

5.1 Experimental Investigations of The Causation of Fear-Like Responses to Male Conspecifics

5.1 (a) Introduction

Attempts in this laboratory to condition male Bettas to perform a ring swimming operant for aggressive display reward often necessitated the use of a subject selection procedure. The reason for this was that many male Bettas presented with both displaying and non-displaying males would show the pattern of retreats from the opponent described by Bols (1977) as elicited by non-displaying male conspecifics and by de Bruin for a mirror image (1977). The results and conclusions of Bols have already been discussed in detail. Her interpretation of the behaviour elicted by non-displaying males as fear has been questioned on functional grounds, and criticized for its use of only a single method for establishing the behaviour's causation. Her interpretation of the reason for displaying males showing fearful behaviour rests on the hypothesis that non-displaying is contrary to the expectancies of subjects. This implies that displaying males expect their display to be reciprocated by the receiver. If this is so, it is difficult to understand the occurrence of fear-like behaviour to mirror image stimulation reported by de Bruin (1977). He interprets this behaviour not in terms of fear, but as representing a low level of aggressive motivation.

Observations in this laboratory when attempts were made to condition Bettas using display eliciting live conspecifics suggested that although submissive (non-displaying) males elicited more fear-like behaviour than displaying males, it could be elicited by both types of stimulus. Since this behaviour has been interpreted in different ways by de Bruin and Bols, and since it can occur during operant experiments and can be a major source of inter-subject variability in display and operant performance, it may be important to discover the causation of fear-like responses to male conspecifics. The following series of experiments investigates

the causation of fear-like behaviour and begins by comparing the behaviour elicited by displaying and non-displaying (subordinate) males. On the basis of Bols' results, subordinates should produce more retreat-like behaviours than displaying males.

5.1 (b) Habituation of Display - A Methodological Problem

Since the implications for display in Betta splendens of the use of models or mirrors as display eliciting stimuli have never been fully assessed, all the experiments reported in this thesis use live conspecifics to elicit display. Certain problems may however be anticipated.

Several studies involving repeated aggressive encounters in males of a range of fish species report the waning of aggressive responding over the series of tests (for Betta splendens: Baenninger, 1966; Peeke and Peeke, 1970; Klein, Figler and Peeke, 1976; for convict cichlids (Cichlasoma nigrofasciatum): Gallagher, Herz and Peeke, 1972; and for sticklbacks: van den Assem and van der Molen, 1969; Peeke, 1969 and Peeke and Veno, 1973, 1976). In the operant situation, with display rewarded Betta splendens, reward rates on continuous reinforcement schedules may be thirty per hour for mirror image stimulation (e.g. Thompson, 1963; Goldstein, 1967) or higher (e.g. Hogan, Kleist and Hutchings, 1970). For live conspecific rewards, rates at least this high were to be expected and this would imply a total reward exposure time of at least 15mins. per daily one hour session.

Peeke and Peeke (1970) presented male Bettas in their home tanks with live male conspecifics enclosed in glass containers. Daily 15min. presentations resulted in a significant decline in "aggressive display" (lateral display) "maximal aggressive display" (gill covers erect and sometimes including lateral display) and biting by the ninth day of testing. Biting did not occur from the sixth day to the twentieth. A second group of subjects was presented with male conspecifics for a single 1hr. period on 5 consecutive

days, a total exposure time equal to that of the first group. Habituation was found to be slower and qualitatively different in terms of the order in which display components declined. Even with this procedure, "maximal aggressive display" declined significantly within the first session. Baenninger, Bergman and Baenninger (1969) reported that habituation occurs even when 15min. tests were held once weekly. For mirror image stimulation they found that all of their 9 subjects displayed during test 1, but by test 7 (7 weeks later) only 2 fish displayed. A decline in responsiveness to displaying male stimulus fish was also found.

In the operant situation, habituation also occurs. Rhoad, Kalat and Klopfer (1975) found that operant responding in male Bettas declined over sessions for several reward stimuli, including a live conspecific male. They remark that a decline in display during reward also occurred. Bols (1976) used displaying and non-displaying male conspecifics as rewards for male Bettas in an instrumental learning situation and found that instrumental performance for the non-displaying males declined over sessions.

The rate at which aggressive display wanes with repeated elicitation is related to the strength of the stimulus as a display elicitor. Figler (1972) reports that for gill cover erection duration and fin erection duration (frontal and lateral display respectively, in the present thesis) the absolute decrement which occurred over sessions was positively related to the strength of the eliciting stimuli. However, the proportion of decrement which occurred over sessions was inversely related to the eliciting strength of the stimulus.

For Betta splendens aggressive display it might be expected from the above that habituation of the display would occur over many stimulus presentations. It might also be expected that the stimulus which responds least to the actor, and which is therefore most predictable (a submissive male) would produce habituation to a greater degree (in terms

of absolute decrement) than a responsive displaying conspecific. Since the likelihood of habituation to the rewarding stimulus must be reduced as much as possible, an unconventional means of stimulus presentation will be used in the experiments to be reported here. Since Betta splendens is territorial while in reproductive condition, and since whether in reproductive condition or not, isolated male Bettas defend their entire visual field, the presentation of the conspecific unambiguously inside the territory may reduce the effects of habituation. For this reason instead of being visually presented through a tank wall as in Rhoad, Kalat and Kopfer's (1975) experiment, the conspecific stimulus is presented in a glass container inside the subject's home tank, and this presentation can be terminated by masking this container with a cylindrical opaque cover which may be raised and lowered. This situation may be considered midway between that which Lobb and McCain (1976) call "mutual viewing" and the unrestrained situation which they term "mutual cageing".

The potential methodological problem of habituation to the reward stimulus may be assessed in the same experiment as the theoretical question of the differences in display to displaying and non-displaying male conspecifics.

5.2 Responses to Displaying and Subordinate Males - Experiment 1.

5.2 (a) Subjects

Eight male Betta splendens were randomly selected from those kept under initial maintenance conditions (described in 4.1 (a)). These eight males acted as experimental subjects. Each subject was then assigned two stimulus fish, one which displayed and one which was subordinate.

5.2 (b) Conspecific Stimuli

For each subject two stimulus males were chosen from stock,

one which displayed aggressively and one which showed the subordinate posture and markings described in ch. 2.7. The displaying stimulus termed the "rival" and the subordinate was termed the "subordinate". Rivals and subordinates were chosen from the remaining stock of male Bettas by the following procedure:

A male Betta in its home tank was caught by means of a dip net and gently placed in the stimulus container filled with water from that male's own home tank. The fish was immediately fed and left undisturbed for 5mins. After this period of recovery from the netting procedure the container with the fish inside was gently placed in the centre of the home tank of one of the subjects. After the subject's first approach (to within one fish length) to the stimulus fish container the behaviour of the stimulus fish was observed for 3mins.. If it displayed aggressively for the full 3mins. it was designated the "rival" for that subject. If it showed subordinate markings and posture it was designated the "subordinate" for that subject. If the stimulus made a transition from displaying to non-displaying or vice versa, or if behaviour not easily classifiable occurred (such as maintaining medial fin erection and dark coloration while thrashing about within the container with escape-like movements) then this fish was rejected as a stimulus for all subjects. In the case of rejection of a stimulus fish a new male was chosen and the procedure repeated.

When the first subject had been assigned a stimulus male, rival or subordinate, whichever was appropriate, the procedure was repeated for the second subject and so on for all 8 subjects. The first subject was tested with a second stimulus male only after all subjects had one stimulus assigned them and at least 30mins. had elapsed.

A second stimulus male was provided for each subject in the same way as before except that in this case rejection of a stimulus for a particular subject also occurred if that stimulus behaved in the same manner as the first. In

this case stimulus fish were tested with that subject at intervals of approximately 30mins. until the subject had a rival and a subordinate assigned to it. In one case a rival could not be found for a subject and that subject was rejected and a replacement randomly chosen from stock. If a stimulus fish was rejected on the basis of responding in the same way as the first stimulus fish tested with that subject, it was returned to its home tank and not tested with another subject until at least 30mins. had elapsed. This procedure was repeated until all subjects had a rival and subordinate assigned to them.

Two subject fish did not approach and display to any stimulus males available and were rejected and replaced with two males randomly selected from stock. The 8 subjects and 16 stimulus males were then transferred in their home tanks to the experimental maintenance situation described in ch. 4.1(c).

5.2 (c) Experimental Design

Subjects were presented with rival and subordinate stimuli in two blocks of daily 15min. test sessions, a rival block and a subordinate block. The subordinate block consisted of 9 consecutive daily tests. The rival block consisted of 9 consecutive tests or until the rival assigned became subordinate, whichever occurred first.

The 8 subjects were randomly divided into two groups of 4 subjects each. The first group was assigned the block of subordinate tests first. The second group had the rival block first. Rival and subordinate blocks were separated by a period of 24hrs. during which no testing took place. If a rival became subordinate during a test or did not display in response to the subject's first 3 approaches that rival was rejected and the rival series for that subject was terminated. Twenty-four hours later the subject began its series of subordinate presentations if it had not already taken place.

5.2 (d) Procedure

At the test chamber, the black cylinder cover was placed over the stimulus container and they were together lowered manually through the test chamber roof cut away, into the subject's home tank. Five minutes later the chamber light was switched on and the stimulus cover was raised by activating the motor. The timer and data recording devices were not activated until the subject had approached to within one fish length of the stimulus container.

The behaviour of both subject and stimulus fish were recorded for 15mins. The motor was then activated to lower the stimulus cover and the chamber light was switched off. Approximately one minute later the stimulus cover and container were manually removed and the stimulus fish returned to its home tank. The stimulus container was then washed thoroughly. The subject's heater thermostat was disconnected and its home tank carried to the maintenance room. Testing of each subject was carried out at approximately the same time each day.

5.3 (a) Differences in Behaviour to Rivals and Subordinates - Qualitative Results

When presented with a rival, males approached with erect gill covers and thereafter stayed close to the stimulus fish, alternating between frontal and lateral display. Lateral display was often accompanied by tail beating and frontal display sometimes gave way to butting. As the encounter proceded, butting and biting became more frequent.

In marked contrast to this behaviour which involved the subject remaining in close proximity to the stimulus fish, the presentation of subordinates produced a series of "visits" to the stimulus initiated by an approach and terminated by a withdrawal. During a visit alternations between frontal and lateral display occurred, grossly similar to those elicited by a rival. However, this period was often of very short duration involving only single bouts of frontal

and lateral display immediately followed by a withdrawal from the stimulus. While away, the subject would swim with undulatory movements and interspersed this swimming with stops with medial fins erect and wall swimming. These behaviours will be referred to collectively as withdrawal behaviours. These were followed by a further approach to the stimulus, usually but not always with gill covers erect, for another visit of frontal and lateral displaying. Tail beating usually occurred during lateral displays. Butting and biting to a subordinate were rare and when bites did occur they often followed particularly rapid approaches and were extremely vigorous.

5.3 (b) Quantitative Results

One subject died after completing the 9 day series of subordinate presentations but before the first day of the rival condition. Death was due to a heater thermostat failure. Data from this fish was ommitted from condition comparisons but retained in analysis solely concerned with responding to a subordinate.

The results of comparisons (Wilcoxon) of the behaviour of subjects on the first day of each condition are shown in Figs. 3 and 4. Subordinates elicited significantly higher frequencies of stops with medial fin erection (StME), wall swimming (Wls), withdrawals (Wi), and undulating swimming (Usw). The subordinate also produced significantly higher durations of StME, Wls, and Usw and significantly lower frequencies of Bi, air gulping (AG) and tail beating (TB) and lower durations of AG. The subordinate produced nonsignificantly lower frequencies and durations of frontal display (FD), lateral display (LD) and butting (Bu).

A striking characteristic of behaviour to a subordinate is the high degree of intersubject variability. Table 1 shows the total durations of FD, LD, Usw, StME and Wls shown to rivals and subordinates by each subject. It can be seen that some subjects (the first three in the table) behave to

subordinate and rival with roughly similar amounts of each behaviour, showing fairly large amounts of FD and LD and very little Usw, StME and Wls. The remaining subjects show to a subordinate large amounts of Usw, StME and Wls with relatively low levels of FD and LD, while to a rival they show large amounts of FD and LD and little Usw, StME and Wls. Only one subject showed nest building and no subject showed nest posting or fanning on the first day of subordinate or rival presentation.

5.3 (c) Discussion

The behaviour elicited by a subordinate in this experiment seems comparable to that elicited by "non-displaying" males in Bols' (1977) T-maze experiment. In that situation, where instrumental and reward-elicited behaviour to displaying and non-displaying stimulus males were compared, the non-displaying reward stimulus elicited more frequent "turning back" in the runway and "air gulping ". It also produced shorter durations of "gill cover erection" and longer durations of "thrashing". If turning back, gill cover erection and thrashing are equivalent to withdrawing, frontal display and wall swimming respectively in the present experiment, then the results obtained here substantially agree with those of Bols. Not in agreement with the present results is her finding of a higher air gulping frequency to the non-displaying male. The opposite result was found here.

On the basis of the behaviour occurring in response to non-displaying males Bols (1977) concluded that more than one motivational system was involved in display reinforcement. She suggests that "fear" is the causal factor underlying the "turning back", "remining motionless" and "thrashing". Why a non-displaying and presumably subordinate male should elicit fear has been questioned earlier (ch. 3.1(b)) and it was suggested that on functional grounds this does not seem likely. Furthermore whether functionally plausable or not, a single line of evidence, in this case the morphology of

the behaviour, is not a sufficient basis for the identification of causal factors. Neverthless Bols' results do suggest that whatever the nature of the underlying motivational systems there are at least two systems operating in response to a non-displaying stimulus. Her observation that "thrashing" bore a roughly reciprocal relation to gill cover erection may as she suggests indicate that the causal factors underlying these behaviours are mutually inhibitory. In the present experiment where a subordinate was the stimulus the behaviours did seem to fall into two groups, one group being the behaviours that occur close to the stimulus (FD, LD, TB, Bi, Bu), and the other being those which occur away from the stimulus and the act of leaving the stimulus itself (Wi, Usw, StME, Wls). Not only as Bols (1977) suggests, does gill cover erection (FD) seem to bear a reciprocal relation to thrashing (Wls) but all members of the first group seem to be negatively related to those of the second group. Within groups positive relations seem to exist such that a subject who shows a high level of particular behaviour will show high levels of the other behaviours of that group and small amounts of all the behaviours of the other group. If Bols' suggestion about the reciprocal nature of the relations between gill cover erection and thrashing can be confirmed, then considerable support would be available for the hypothesis that two mutually inhibitory motivational systems were involved in display to non- displaying male conspecifics. The nature of the two systems (fear, aggression) would still, however, remain an open question demanding a different kind of evidence. The following analysis attempts to gain insight into the nature of the relations between the various subordinate elicited behaviours.

5.4 The Relations Between Subordinate-Elicited Behaviours

5.4 (a) Introduction

If as Bols (1977) suggests, two mutually inhibitory systems are involved in the control of subordinate elicited

behaviour, then negative correlations may be found to exist between behaviours controlled by one system and behaviour controlled by the other. Both Bols' suggestions and the qualitative description of behaviour to a subordinate given earlier, indicate that behaviours may fall into two groups, those behaviours occurring within a fish length of the stimulus and those occurring away from it.

If all the behaviours occurring close to the stimulus (Bi, Bu, FD, LD, AGd) share common causation then they may be found to be positively intercorrelated. Similar reasoning holds for the behaviours away from the stimulus (Wi, StME, Usw, Wlsw). Correlations between behaviours occurring close to and those occurring away from the stimulus should be negative if they are controlled by mutually inhibitory systems. No predictions about the sign of intercorrelations will be made about air gulping frequency since it occurs both near and away from the stimulus. However, since protracted air gulps (i.e. longer than one second) occur only close to the stimulus, AG duration should be positively correlated with other behaviours which occur during visits. It must be pointed out that these hypotheses do not assume that where negative correlations exist between behaviours they must necessarily be due to inhibitory relations between the underlying systems.

5.4 (b) Method

Spearman Rank correlation coefficients were computed between all measures of every behaviour and every other behaviour occurring on the first day of presentation of a subordinate. The correlations (N=8) are based on total amounts of each behaviour in individual subjects and computed over subjects. Since predictions have been made about the signs of correlations between behaviours, significance testing is 1 - tailed, except for AG frequency about which no directional hypothesis has been advanced.

5.4 (c) Results

Table 2 shows the resulting correlation matrix. The most striking thing about this matrix is that ignoring the significances of correlations there are clearly two groups of behaviours. Those within each group are positively intercorrelated and are almost all negatively correlated with behaviours of the second group. As predicted, the behaviours occurring close to the subordinate (FD, LD, TB, Bi, Bu, AG duration) are positively intercorrelated and may be termed the approach group since they follow an approach. The second group of positively intercorrelated behaviours are those occurring away from the stimulus (Wi, StME, Wls, Usw). This group may be termed withdrawal group. Behaviours of the approach and withdrawal groups are almost always negatively correlated. Air gulping frequency falls into the withdrawal group while AG duration falls into the approach group.

The significance of the correlations are also presented in Table 2 and from these it can be seen that Bi, TB, AG duration and frequency are the only behaviours not significantly correlated with any other behaviours.

5.4 (d) Discussion

The existence of two major groups of behaviours with negative relations between groups does suggest that at least two major causal variables are operating, and that the relations between these variables may be inhibitory. It is not, however, being suggested that all the behaviours within a group are caused by the action of a single unitary "drive". Hinde (1959) has pointed out the serious limitations of drive models of motivation and these have been discussed in ch. 3.3. It is generally accepted however that at the early stages of the causal analysis of a behaviour the conceptualization of the motivation underlying a group of behaviours in terms of drive like entities can be useful.

So far the indentification of two behaviour groupings possibly mutually inhibitory is consistent with Bols' (1977) interpretation of the behaviour she observes in response to a non-displaying conspecific. If the system underlying withdrawal behaviours were a fear system, or if the occurrence of these behaviours indicated the temporary dominance of a fear over an "aggressive" tendency or drive, then negative relations between withdrawal and approach behaviours would be expected and this result has been found. Again it must be pointed out that the evidence available is as yet insufficient to identify the nature of the causal factors underlying withdrawal behaviours.

5.5 The Course of Display With Repeated Presentation of A Rival

As described in 5.2 (c), it was intended that each subject should be presented with each stimulus for nine consecutive days, allowing the detection of any changes of behaviour which might occur with repeated presentations of the stimuli. It was expected that a non-displaying stimulus fish would produce a more rapid decline in the subject's display due to the predictability of its behaviour. Such comparison is not however possible because only one displaying stimulus fish continued to display for the entire nine days the rival series, while the rest became subordinate. All but one of the males who became submissive did so between sessions. That is, a session in which the stimulus fish displayed normally, would be follwed by a session (the next day) in which it did not even begin to display. Interestingly this occurrence could often be predicted from the behaviour of the fish on being placed in the stimulus container. If it showed submissive posture and markings at that point it was unlikely to display when presented to the subject.

Some suggestions can be made about the probable cause of this dominance establishment. One possibility is that the test sessions are to some degree aversive to the stimulus fish, perhaps because dominance over it was slowly being

established and being placed in the stimulus container became a cue for the forthcoming aversive situation. The second possibility is that as test sessions proceed, perhaps due to the social stress involved, the stimulus fish is subject to a gradual lowering of a fright threshold. This might result in the netting procedure producing a fright response which it was not previously aversive enough to elicit. This might also explain why it was always the stimulus fish which became subordinate rather than subjects. However, other hypotheses can be advanced to account for this latter observation. For example, the subject during the aggressive interaction, regularly swims circularly around the stimulus fish in lateral display or while butting. The stimulus fish can only respond to this by adjusting its own orientation, because being confined in the stimulus container it cannot swim around the subject. The implication of such a constraint for the communicative processes involved in display (see Simpson, 1968) may be considerable.

Since five subjects had a stimulus fish which displayed to them for two sessions or more it is still possible to ask whether these relatively few sessions reveal any tendency for displaying to decline with repeated stimulus presentations.

5.5(a) Results

Considering first the overall responsiveness of subjects to rivals over daily sessions, the total time spent performing all behaviours whose durations are measured was calculated. Table 3a shows that three of the five subjects tested for two days or more actually increased the total time spent performing the behaviours observed. These account for approximately 84% of the total test time, the remainder being spent in behaviours whose frequency only are recorded or in behaviours not recorded at all. An example of the latter which may occupy a substantial amount of time is swimming round the stimulus fish in neither frontal nor

lateral display which often occurs before a bout of biting. This behaviour involves swimming facing the stimulus fish but without gill covers erect and without butting.

Considering the individual behaviours elicited by rivals Tables 3b and 3c respectively show that lateral display duration and frequency show no progressive decline over sessions and LD duration actually increases in three of the five subjects. Frontal display frequency does not decline consistently across subjects (Table 3d) but frontal display duration decreases in four of the five fish (Table 3e). In contrast, butting frequency (Table 3g) and duration (Table 3g) increase over sessions, as does biting frequency (Table 3h). Air gulping frequency (Table 3i) and duration (Table 3j) show no consistent pattern.

5.5 (b) Discussion

No evidence has been found to suggest that an habituation process was operating before dominance was established by subjects over their rivals. Only a single display component, FD duration, decreased reliably over sessions and this may be explained by the increase in butting which occurred. Butting follows a frontal display and is often followed by it. If the tendency to butt increases, frontal display may be the behaviour over which it takes precedence.

The increase over days in butting and biting may reflect a gradual increase in attack tendency such as that described for the cichlid (Haplochromis burtoni) by Heiligenberg and Kramer (1972). An alternative interpretation in this context might be a reduction in inhibitory factors by increasing familiarity with the opponent or by the learning by subjects that they cannot be actually bitten by their rivals. The possibility that familiarity with the opponent may increase attack by disinhibition could be investigated by switching opponents during series of daily encounters.

These results suggest that the methodological problems associated with habituation for the use of live conspecifics as rewards in an operant situation,may not be as severe as was anticipated. Rather more difficulty may be caused by the occurrence of dominance. It has already been suggested that this may be facilitated by increasing aversiveness to stimulus fish of the netting procedure before testing. For operant experiments, an attempt will be made to reduce this by increased care in the execution of all pre-test procedures. The strategy which will be adopted in operant experiments will therefore be to minimise factors likely to lead to dominance where possible, and when it does occur, to simply replace stimulus fish. In the present experiment 4 of the 7 subjects did not produce submission in their rivals before 4 sessions had been carried out. This would be sufficient time for the collection of an adequate amount of operant data if the response was already aquired.

5.6 The Course of Display With Repeated Presentations of a Subordinate

5.6 (a) Results

Table 4 shows the course of mean FD, LD, AG, Bu, Usw, StME. Wls, Bi and Wi frequencies over the 9 days of the subordinate condition. No significant change occurred over sessions (Friedman two-way analysis of variance). Table 5 shows the durations of these behaviours (if recorded) and the total durations of recorded behaviours over days. Only AG showed a significant change over sessions (Fried., $p<.05$). All 8 subjects showed a decrease in AG duration from Day 1 to Day 2, remining at a stable level thereafter.

5.6 (b) Discussion

Only for the duration of air gulping was any evidence found of habituation to a subordinate. Inspection of mean AG duration over sessions (Table 5) reveals however that the

form of the decline was not what would be expected of an habituation process. Instead it seems an effect specific to the first day of subordinate presentation, i.e. due to the beginning of the experiment, or a change in stimulus from rival to subordinate.

As mentioned earlier, intra-individual variability is very great in the subordinate condition and this remains true over the nine days of presentations. If this variability is thought of as variability in the relative strength of two major motivational factors associated with the behaviours identified earlier then some clue about the causation of withdrawal behaviours can be derived from the course of one individual's behaviour over days. This particular subject showed an interesting transition from spending most time in withdrawal behaviours, (Wls, Usw and StME) on Day 1, to Day 9. Fig. 5 shows the course of this change in withdrawal and approach behaviours over sessions. The occurence of such a transition, since no obvious change in the behaviour of the stimulus occurred, may be attributed to an internal change in the subject. One possible change in internal state whose effects on aggressive display in previously isolated Betta splendens have not been investigated is the reproductive cycle. An indication of a male Betta's reproductive readiness may be gained from his nest building behaviours (discussed in ch. 2.5). Fig. 5 also shows that in the individual mentioned, preceding the change in the relative amounts of the two types of behaviour was a transition from having a nest to not having one. Furthermore, when records of nest building in each subject was examined for the first day of subordinate presentation, of the three subjects whose behaviour was similar to that shown to a rival (see Table 1) two did not have nests, and the remaining one had only a very small, ill developed aggregation of bubbles. The remaining four subjects which show large amounts of withdrawal behaviours had nests at fairly advanced stage of construction.

The possibility that sexual tendencies may be involved

in the motivation of withdrawal behaviours is further supported by the observation that some subjects showed nest posting during subordinate presentations. Five subjects showed NB at some time during the nine days and four subjects showed NP. Fanning (Fan) was never observed. Nest related behaviours were never seen in the rival condition.

5.6 (c) Subordinate Elicited Behaviour and Courtship

In a sexual encounter (described more fully in ch. 2.7) approaches to the female with frontal and lateral display are followed by leading the female to the nest with what Simpson (1968) has called vivid swimming. A reproductive female will follow and will ultimately be driven away. In the present experiment where the male subordinate stimulus can neither follow nor escape, the similarity of the behaviours to normal courtship is far from complete. Nevertheless, the possibility still exists that an aberrant form of courtship behaviour is here being shown to subordinate males, whose nature has not been recognised because the constraints of the situation have modified its form. This suggestion raises the possibility that subordinate males have elicited inappropriate behaviour in some subjects, that is, they have been treated as reproductive females. This demands some consideration of the mechanisms of sexual discrimination in the males of this species.

5.7 Cues For Sexual Discrimination in Male Betta *splendens*

In an attempt to discover the basis of sexual discrimination in male Bettas, Robertson and Sale (1974) compared males' behaviour to live conspecifics of each sex, and a series of models differing in body markings and the sex they represented. Two of these models were "lifelike", one of an unripe reproductively marked female and the other of a male in "broadside display" (both lateral display and gill covers erect). Of the remaining six models half represented males and half

represented females. These included a male and female in "aggressive display" a pair with "submissive" markings, i.e. horizontal stripes, and a pair with reproductive markings, i.e. with vertical bands. Apart from the differences in markings submissive and reproductive males were identical to the aggressive male, having raised opercula and medial fins. In addition,behaviour to live conspecific males (displaying) and females was compared.

As in the previous experiment two groups of behaviours emerged from interbehaviour correlations. One group was termed "agonistic" and occurred close to the stimulus and the second was termed "nest oriented" since the behaviours away from the stimulus were closely associated with nest related behaviour. Within groups of behaviours correlations were positive, and between groups they were negative. Following this a factor analysis was performed yielding three factors. The first was described as a tendency to perform agonistic display and inhibit nest activities. The second factor was described as a tendency to raise the opercula and to tail beat, and the third to approach and to bite. Robertson and Sale concluded that the difference they found in response to the various classes of stimuli were differences in the relative tendency to perform agonistic and nest oriented activities. When the stimulus was a female they suggest that the factor underlying agonistic behaviour is weak and the likelihood of performing nest related behaviour is consequently strong. Furthermore, they present evidence suggesting that no difference exists between male and female stimuli in the second and third factors and that these may be a general response to the stimulus as conspecific, as distinct from specifically male.

The response to the models fell into two groups with that to lifelike, submissive and reproductive male models being most like the response to the live male and that to the lifelike submissive and reproductive female models being most like to response to the live female. The effect of markings on male models (submissive and reproductive)

served to shift the response more in the direction of the female elicited behaviour. On the basis of these results they suggest that the mechanism of sexual discrimination in male Bettas is based on visual differences between stimuli, with long fins and unpatterned bodies being most likely to elicit agonistic behaviour than models with patterned bodies and short fins. Several difficulties of interpretation are associated with this conclusion however. Firstly they did not directly compare the effect of long or short fins on an otherwise identical body. The body shape of females who all had short fins were different from the body shape of male models who always had long fins. The effect of long fins alone was not therefore investigated directly. Secondly, all models of males had erect medial fins and raised opercula, even those with submissive markings. Even two of these characteristics are rarely seen simultaneously in live males and their combined effect on male behaviour is thus difficult to interpret.

Robertson and Sale suggest that support for their conclusions comes from the observation that when two of their live conspecific males ceased to display and became submissive they were immediately treated much more like females. That is, the change in their visual aspect from raised opercula, unpatterned body and long fins to short fins, patterned body and lowered opercula fully accounts for the subject's subsequent changes in behaviour. Other findings of theirs are however inconsistent with this conclusion. For example, two of their subjects behaved to a displaying male conspecific as they would to a female. In addition seven of their subjects treated aggressive female models as males. They also remark that the males who treated models differently from the way the majority treated them were more likely to "court" a male than threaten a female. This suggests that the conclusions drawn were based on highly variable behaviour and the suggestion of a fairly simple visual discrimination on the basis of a small number of "criteria" may not adequately account for the complexity of the process.

That a female Betta with lowered opercula short fins and unpatterned body will often be treated as a male, that is responded to agonistically, has been observed repeatedly in this laboratory when mixed sex groups are housed in large tanks. This aggressive response to a female most often occurs in the early stages of territory establishment by the male. If a female approaches the male, frontal and lateral display will be elicited if she does not immediately flee. It seems also that where females elicit less agonistic display than males it is only because they often retreat sooner, which is probably associated with being smaller and themselves not being motivated to establish territories. After a territory has been established for some time by a male and usually after a nest has been built, a female previously attacked will be immediately courted if she intrudes into the territory. The possibility therefore exists that, to a female, at least, a male's behaviour may depend on his position in the reproductive cycle. This may also be the case with male stimuli. Robertson and Sale consider the possibility that the criteria for sexual discrimination in males may change over time but reject this as unlikely,

"...as long as the fish remain in good physical condition".

With reference to the experiment reported here in which displaying and subordinate males differed in the behaviour they elicited, it can be asked whether this is explicable in terms of a failure of sexual discrimination such that subordinate males are courted.

The suggestion that withdrawal behaviours are sexually motivated can be tested by the experimental manipulation of the supposed underlying tendency (see ch. 3.2). That is, if the underlying causal factor is sexual, then the behaviour should be altered by manipulations of the sexual tendency directly or indirectly. Evidence for the causation of those behaviours would then be obtained independently of their morphology. In the context of the last experiment

it was suggested that whether or not the male Betta possessed a nest might be an indicator of its reproductive readiness or the strength of its sexual tendencies. This means that by taking groups of males, one group having built nests and the other group without a nest and presenting both groups with subordinate males, the effect of an underlying reproductive state or sexual tendency on display behaviours could be assessed.

5.8 The Effect of Reproductive Conditions on Behaviour to A Subordinate

5.8 (a) Experiment 2 - Introduction

The following experiment is based on the premise that courtship behaviours would be expected to vary in concert with nest building. It has been mentioned earlier that the nest building of Betta splendens males is cyclical (de Bruin, 1977), and the strength of the motivational states underlying courtship would be expected to follow similar patterns. If the withdrawal behaviours observed in some males when presented with a subordinate are variants of sexual behaviour, then males in nest building conditions would be expected to show more of these behaviours than males who are between peaks of the nest building cycle. The following experiment therefore compares the behaviour of nest building males and males without nests in their behaviour to a subordinate.

It was hypothesised that males with nests would show higher frequencies and durations of the withdrawal group of behaviours (Wi, StME, Usw, Wls, Fan, NP, NB and AG frequency) and since approach and withdrawal behaviours have been shown to be negatively correlated they should show less of the approach group of behaviours, (FD, LD, Bi, Bu, TB and AG duration).

5.8 (b) Subjects

Two groups of 7 male Bettas each, a "nest" group (N)

and a "no nest" group (XN), were selected from the stock of experimentally naive males kept under initial maintenance conditions. The N group was selected randomly from those having at least one aggregation of bubbles on the surface of their home tanks whose volume exceeded 1.0cms^3. The XN group was randomly selected from those males having no aggregation of bubbles of an estimated volume greater than 0.4 cms^3. Nest measurement was achieved by holding a transparent perspex plate marked with a grid of 1cm. squares over the nest. The number of squares the nest occupied was counted with the nest areas of less than half of a square being ignored and over half of a square being counted as 1cm.^{2} Nest height was considered to be the maximum height reached by the nest at any point and was measured by holding a ruler vertically against the outside of the tank wall. The volume of the nest was then extimated by multiplying its maximum height by the area of water it covers. This method leads to an overestimation of the volume of peaked or conical nests. However, the criterion for nest presence used seemed to be an appropriate one since subjects who exceeded the criterion for inclusion in the N group usually did so by a large amount, and subjects allocated to the Xn group rarely had any aggregation of bubbles at all.

The two groups of selected subjects were transferred to experimental maintenance conditions and kept there for one day before testing. On the day of each subject's testing the mean nest size of the N group was 14.16cms.^{3} (S.E.= 5.5cms.^{3})

5.8 (c) Stimulus Fish

Three male Betta splendens were chosen from those used as subordinates in the previous experiment. These subordinates had not been presented to the present subjects at any time before the experiment.

5.8 (d) Apparatus

The same apparatus was used in this as in the previous experiment.

5.8 (e) Procedure

Subjects were tested for 15mins. with each of the three subordinates on a single day. Within a subject the three tests were separated by a period of 60mins. The order in which stimuli were presented to subjects was counterbalanced for 6 subjects of each group with the extra two subjects (one from each group) having stimuli presented them in random order. Only one subject was tested per day and the order of subject testing was randomly determined without reference to group. The preliminary and testing procedures were the same as for the previous experiment.

5.8 (f) Results

Not every subject in either experimental group could be tested with all three subordinates since all stimulus fish displayed aggressively to some subjects, one displayed to three subjects, another displayed to two subjects and the third displayed to one subject. The subordinate who most often displayed aggressively was also the largest of the three stimulus fish. No subject was displayed to by more than one subordinate, and subordinates displayed most often to members of the XN group (four occasions against two). Each subject was therefore tested with either two or three subordinates and for group comparisons the mean of these two or three tests was used giving one value for each behaviour for every subject. Significance testing of group differences was by Mann-Whitney U test. Since directional hypotheses have been advanced, 1 - tailed probabilities are reported.

Figs. 6-10 indicate that the XN group showed a significantly higher frequency of butting and significantly higher durations of frontal display, lateral display and butting than did the N group. XN subjects also showed significantly lower frequencies and durations (where applicable) of undulatory swimming, stops with medial fins erect, wall swimming, nest building, nest posting, fanning, withdrawing and tail beating. Although XN subjects did show higher mean frequencies of frontal and lateral display than subjects of group N, as predicted, the difference

only approached significance (Mann-Whit. U, P>.10). Group differences in bite frequency, air gulp frequency and air gulp duration were also not significant.

The effect of differences between stimulus fish on the display of subjects was assessed by comparing the behaviour of subjects to the three subordinates irrespective of those subjects' grouping. Since only eight of the fourteen subjects were tested with all three stimulus fish, only these eight are used in the stimulus comparisons. Tables 6 and 7 show that the 3 different stimuli produced no significant differences in the frequencies or durations of any recorded behaviour (Friedman).

For the same eight subjects used above for stimulus comparisons, the effect of the serial order of testing was investigated by comparing each subject's behaviour to the 1st, 2nd and 3rd stimulus fish presented to it, irrespective of stimulus fish identity. Tables 8 and 9 show that the serial position of a test had no effect on any recorded behaviours in that test. Only the increase in nest building duration over successive tests even approaches significance (Fried., P>.20).

5.8 (g) Discussion

Males with nests showed significantly more of most withdrawal behaviours and less of most approach behaviours than males without nests. Earlier, it was suggested that the causal factors underlying withdrawal behaviours may be sexual and when they are shown to subordinates they may be, functionally speaking, misdirected sexual behaviour. The finding that withdrawal behaviours are dependant on males' nest building state for their occurrence will be taken as non-morphological evidence of the sexual causation of these behaviours. Furthermore in the present experiment overt nest-related behaviours did occur associated with withdrawal behaviours in the nest owning group.

The finding of a relation between nest ownership and withdrawal behaviours must be considered inconsistent with Bols' (1977) interpretation of these behaviours as caused by escape tendencies. If any relation between escape tendencies and nest building were expected this relation would be more likely to involve a decline in fearfulness accompanying nest building and territory defence, with a rise in aggressive tendencies.

An alternative interpretation of the withdrawal-nest building relation is however possible. It may be that the nest related activities observed to occur in the nest group were stimulated by the actual presence of the nest itself, (see ch. 2.5) and that withdrawal behaviours reflect some kind of conflict between the tendency to approach and display aggressively to the male stimulus, and the tendency to stay near the nest which may be the centre of the territory. The behaviours, Usw and StME may be vacillatory swimming movements. This suggestion implies that a general state of sexual readiness which manifests itself in nest building does not directly cause withdrawal behaviours to a subordinate male but instead, these behaviours occur under the influence of the actual presence of the nest. A further experiment is therefore required which controls for this possibility by comparing the subordinate elicited behaviours of males who have constructed nests and whose nests are actually present, with the behaviour of males whose nests have been experimentally removed.

Some comments about the relationship between display and attack behaviours may be made on the basis of a comparison between the results of the present experiment and those of the last. In Experiment 1 in which behaviour to rivals and and subordinates was compared, wide variation was found in all subordinate elicited behaviours except biting. That is, however much FD and LD a male showed to a subordinate, it would still bite infrequently. The present experiment revealed two groups of subjects: One group showing a great deal of FD and LD and the other showing very little, but

both groups biting at roughly the same very low frequency. In the XN group, the mean amounts of FD and LD to a subordinate (209.8 and 314.8 secs.) are comparable to the amounts shown to displaying rivals by subjects in the last experiment (253.8 and 306.5 secs.), however the mean frequency of biting in the present experiment for subjects of the XN group (1.19 bites) is markedly lower than that to rivals in the previous experiment (15.86 bites per subject). Although comparisons across experiments are of limited value the above does suggest that the tendency to bite may be lowered by some aspect of the subordinate stimulus. A stimulus characteristic of the subordinate likely to be involved in the reduction of conspecifics' attack tendencies is the presence of horizontal dark bands on the flank. These bands, whose appearance precedes flight in both sexes, appear in conjunction with the paling of body coloration, the folding of the medial fins and the raising of the head so that the body axis is about 30° from the horizontal. When displayed to, the submissive fish retreats slowly, keeping one flank with stripes oriented towards the dominant fish. If at any time during this withdrawal the subordinate fails to maintain this orientation to the dominant animal it will almost always be chased and bitten.

The role of subordinate markings seems particularly clear during courtship. While the male is leading the female towards the nest, he often does perform short frontal and lateral displays. The female at this point is progressively darkening in coloration and showing vertical dark bands on the flank. It may be that the males' own high level of sexual motivation inhibits his attack even though the female shares at least one characteristic of the intruding male, namely dark coloration. However, if the male does procede to attack the female, which sometimes occurs when the female is slow to approach the nest, she rapidly pales in colour and shows submissive horizontal bands identical to those shown by males. This will usually be accompanied by her retreat from the nest area. As in the case of the submissive male a slow retreat with the striped flank presented seems

to lower the likelihood of being attacked.

That body patterns in one fish may reduce or inhibit the tendency to attack in conspecifics has been shown for several fish species. Leong (1969) using models differing in body markings showed that in the cichlid Haplochromis burtoni, the orange patch above the pectoral fins decreases the tendency to bite in other fish. Heiligenberg (1964) considers that the red abdomen of female Pelmatochromis subocellatus kribensis inhibits male attacks, and Wickler (1966) has suggested that in Tropheus spp., the yellow-orange band on the abdomen inhibits biting in both sexes.

An important question about the effects of body markings on the probability of being attacked is whether such markings inhibit attacks which would be directed at the bearer of the markings, or whether their effect is a general one of lowering the probability of the receiver of the signal attacking any fish. Leong's (1969) experiment demonstrated that the reduction in the probability of attack was in fact a reduction in the tendency to attack any conspecific and that this effect lasted for some time after the presentation of the stimulus was terminated. Whether Betta splendens submissive markings have a similar effect on the attack tendency of conspecifics could be ascertained by experiments in which a series of presentations of an attack eliciting stimulus, (a displaying male) which would produce a steady increase in the rate of attack behaviours (see ch. 6), were compared with similar series of presentations interspersed with presentations of dummies with striped markings. The effect of submissive markings could then be assessed in terms of any discrepancy between the actual rate of attack produced and an expected rate, i.e. the rate without dummy presentation. This method would be a modified version of that used by Heiligenberg et al.(1972) in investigations of similar effects in Haplochromis burtoni.

Returning to the present experiment, it was suggested earlier that one reason why the withdrawal pattern of behaviour elicited by subordinates in nest owning males was

not immediately identified as courtship behaviour may be that constraints were placed by the test situation on their behaviour such that it little resembled naturally occurring courtship. Where in an unrestrained interaction between male and female, the male would lead the female towards the nest and that female would follow, the test situation used did not allow such following to occur, and the pattern of the behaviour of leading was therefore quite different. If it can be shown that in the test environment, a male Betta behaves in a similar fashion to reproductive females and subordinate males who differ markedly from such females in appearance, then further evidence would exist to support the suggestion that withdrawal behaviours are courtship behaviours. The following experiment investigates the role of nest presence in the causation of withdrawal behaviours to subordinate males and compares the behaviour of subject to submissive males and reproductive females in the test situation.

5.9 The Effect of Nest Presence on the Behaviour of Males to Subordinate Males, and a Comparison Between Behaviour Elicited by Subordinate Males and Receptive Females

5.9 (a) Introduction to experiment 3.

To investigate the effects of nest presence on withdrawal behaviours, males who had not built a nest could be given nests constructed by other males. However, the insertion of nests into the tanks of male Bettas without nests, can stimulate that male to nest build and to adopt the present nest as his own (see ch. 2.5). The actual presence of a nest may also induce the male to perform sexual behaviours when presented with a female. For these reasons instead of providing non-reproductive males with nests, the following experiment will investigate the effect on withdrawal behaviours of the removal of the nest from the tank of the male which built it, leaving that male without a nest but still in the motivational state which led to its construction.

The comparison made was therefore between the behaviour of nest building males with their nests intact (group N) and nest building males with their nests removed (group NR). Both groups were tested with a male subordinate. The expectation according to the "nest presence" hypothesis was that males with intact nests would show more of the withdrawal group of behaviours (Wi, Usw, StME, Wls , Fan, N B and N P) and less of the approach behaviours (FD, LD, Bu, Bi, TB, and AG duration).

In addition to the comparison between N and NR conditions, a second comparison was made between the behaviour of males of group N (nest present and subordinate male stimulus) and the behaviour of a group of males with their nests similarly intact but who were presented with a reproductive female (group NF).

5.9 (b) Subjects

Twenty-four male Betta splendens were randomly selected from those experimentally naive males kept under initial maintenance conditions and having nest volumes exceeding 1.0cms.^{3} in volume. These subjects randomly allocated to 3 groups; a nest removed (NR) group and 2 nest intact (N) groups. Each of these 3 groups had 8 subjects. The selection, transfer to experimental maintenance conditions and testing of subjects was over several days and the selection of subjects for testing on any particular day was random.

5.9 (c) Conspecific Stimuli

a) The Subordinate Male:
This male was selected from the 3 subordinates used in the previous experiment as being the male who displayed aggressively to fewest subjects.

b) Receptive Female:
Eight female Bettas were obtained from a local supplier and kept together in a large (20 gal.) communal tank for a period of 2 weeks. A nest building male Betta was then netted in its home

tank, placed in a glass container partly filled with water and the container was floated in the females' tank. This procedure served to bring some of the females into reproductive condition as indicated by their dark coloration, vertical black bands on their flanks and gold coloured ventral surfaces. The largest of these females was chosen as a stimulus female because large females are unlikely to be submissive when courted or displayed agonistically to by males. This female was then netted and placed in a home tank similar to those in which males were kept. The male which had brought the female into reproductive condition was then itself poured from its container into that of the selected female. The behaviour of the female was then observed and found to be similar to that described in ch. 2.7, confirming its sexual receptivity. The male was then removed and returned to its home tank. The selected female serves as the stimulus female for males of group NF. Subject males and the subordinate and female stimulus fish were then transferred to experimental maintenance conditions. The apparatus was the same as that used in the preceding experiment.

5.9 (d) Experimental Design

The three groups of subjects chosen were each presented with one of two conspecific stimuli, a subordinate male or a receptive female. The nest removed group (NR) and one of the nest intact groups (groupN) were tested once with a male subordinate. The remaining nest intact group (NF) was presented with a receptive female.

The order of testing of subjects was randomized. The same stimulus fish was used several times on a given day but consecutive tests using the same stimulus fish were separated by at least 60mins.

5.9 (e) Procedure

The preliminary procedure was as described for experiment 1. with in addition the removal of nests from one group of subjects (NR group), by the following method:

Immediately before pre-feeding, a dip net was inserted into the home tanks of NR subjects and the nests were lifted out. The net was rinsed between insertions. The N and NF groups were treated in a similar way, with the dip net being inserted into their home tanks with a movement similar to that used in nest removal for group NR, but the nests were left untouched. The nest volumes of all subjects were estimated again before the preliminary procedure was carried out. Mean nest volumes for each group were as follows:

N; 21.28, (S.E = 6.4cms.^{3}), NR; 24.19, (S.E. = 10.2cms.^{3}), NF; 24.10, (S.E. = 10.2cms.^{3}).

Testing was as for experiments 1 and 2, and as before lasted 15mins. from the first approach of the subject.

5.9 (f) The Effect of Nest Removal on Behaviour to a Subordinate Male - Results

Table 10 shows the results of comparisons between N and NR groups for each behaviour (Mann-Whitney U, 1 - tailed). N.B. NP and Fan rarely occurred and were not subject to statistical testing. No difference in any behaviour was significant in the predicted direction and only FD durations differed significantly when significance testing was 2 - tailed. The only significant effect of nest presence was therefore to produce higher durations of FD. This result, the opposite to that predicted, may be part of a pattern which can be seen in the nonsignificant differences between N and NR groups, such that the N group showed more of the approach behaviours FD, LD, Bu, and TB and less of the withdrawal behaviours Usw, StME and Wi.

5.9 (g) The Effect of Stimulus Fish Sex on the Behaviour of Nest Owning Males

Table 11 shows that no significant differences (Mann-Whitney U, 2 - tailed) were found in any behaviour recorded between nest building males presented with reproductive females (group NF) and submissive males (group N). In contrast the results of the previous experiment, no pattern can be discerned in the directions of the nonsignificant differences between groups.

5.9 (h) Discussion

Since the effect of nest presence on the behaviour of male Bettas to subordinate males is to increase the duration of the approach behaviour FD and not to increase the level of withdrawal behaviours, nest presence cannot be a causal factor in the motivation of the withdrawal group of behaviours. The earlier finding, that nest building males produced more withdrawal behaviours than males who had not built nests, must therefore be interpreted as an effect of nest building tendencies. This finding supports a categorization of withdrawal behaviours to a male subordinate in terms of courtship behaviour and their causation in terms of a sexual tendency or tendencies. Withdrawal behaviours will for these reasons be termed courtship behaviours and approach behaviour will be termed agonistic.

The finding that the gross amounts of behaviours elicited in nest owning males by male subordinates and by reproductive females do not differ significantly may indicate that a failure of sex discrimination is occurring which may be due to constraints imposed on the functioning of sex discrimination mechanisms by the test environment. It must be pointed out however that behaviour to subordinate males and reproductive females may differ in ways not revealed by the present analysis. One such a difference might be in the sequential organization of behaviour. The possible nature of such discrimination mechanisms deserves some

consideration.

Robertson and Sale's (1974) factor analytic investigation of sex discrimination in male Bettas concludes that discrimination is based on visual stimulus differences. It seems implied that the balance between agonistic and nest oriented behaviours is set only by these visual differences and that this effect indicates almost a stimulus response mechanism. It is nowhere considered that whatever visual stimuli are presented by males and females, the effects of these stimuli on behaviour may be mediated by mechanisms whose states are determined by events in addition to the current external stimulus situation. Thus, the effects of a visual stimulus such as long fins, considered important for the identification of a stimulus as male by Robertson and Sale, may be determined by factors independent of the stimulus itself, for example, the reproductive state of the subject male. In addition, Robertson and Sale place little emphasis on the behaviour of the conspecific (other than raised opercula) as a part of the visual stimulus presented by that conspecific. That sex discrimination may be a complex process is suggested by Forselius (1957, p. 409) when he states that,

> "In some Anabantid species, e.g. Betta splendens, the fin movements are of the utmost significance, in others with a marked chromatic sex dimorphism, coloration and movements play an approximately equal part."

He goes on to point out that for Colisa lalia.

> "Also, the male's internal state at the time is, of course, of significance, i.e. at what particular phase of the reproductive cycle the strange fish approaches him ".

For these reasons, Forselius (1957, p. 406) stresses that,

> "...we cannot speak of true 'sex recognition',"

It seems that the reproductive state of a male Betta determines to a considerable degree the way in which it responds to a conspecific, by modifying the effectiveness of that stimulus configuration in eliciting the behaviour

an observer would consider "appropriate". If this were the case, it might be expected that even a displaying male who performs frontal and lateral displays might be courted by a resident male when the resident is in reproductive condition. If both the characteristics of the stimulus and the reproductive condition of the resident are important in determining the resident's behaviour, then it would be expected that as the encounter progressed, under the continuing influence of the stimulus, behaviour would change from predominantly courtship to predominantly aggressive displays. The following experiment investigates the role of nest building tendencies in the behaviour of male Bettas to displaying male conspecifics.

5.10 The Effects of Nest Building Tendencies on the Behaviour of Males to Displaying Males

5.10 (a) Introduction to experiment 4.

From the results of the previous experiments, males with and males without nests would be expected to behave on response to a rival in the following way:

1. Males which have built nests will spend more time in withdrawal beahviours than males without nests.
2. Withdrawal behaviours will decline as the test proceeds due to the inhibiting effect of the rival's display. Approach behaviours will show a concomitant increase.

5.10 (b) Subjects and Stimulus Males

Two groups of 8 male Bettas each, a "nest" group (N) and a "no nest" group (XN) were selected from the stock of experimentally naive males kept under initial maintenance conditions. The N group was selected randomly from those having at least one aggregation of bubbles on the surface of their tanks whose volume exceeded 1.0cms.^{3}. The XN group was randomly selected from those having no bubble aggregations

of an estimated volume greater than 0.4cms.^{3}. Nest measurement was achieved in the same way as in previous experiments (see ch. 5.8(b)).

Two displaying stimulus males were chosen in the same way as described for the stimulus in Experiment 1 (see ch. 5.2(b)). Potential stimulus males were tested with subjects of both groups in counterbalanced order until each stimulus displayed to 4 subjects of each group. Subjects and stimulus fish were then transferred to experimental maintenance conditions.

5.10 (c) Apparatus and Procedure

The same apparatus and preliminary procedure was used in this and in the preceding experiments. Nests of the N group were removed by the method described in ch. 5.9(e), including dummy removal for group XN. Subjects were tested for 15mins. with the displaying male previously allocated to them. As before test sessions began with the first approach of the subject.

5.10 (d) Method of Analysis

Since Experiment 1 showed that withdrawal behaviours were positively intercorrelated and negatively correlated with agonistic behaviours which were themselves positively intercorrelated, analysis of the results of the present experiment will be in terms of the total time spent in the various withdrawal and approach behaviours respectively. The total time spent in each successive minute of the test performing withdrawal behaviours (Usw, StME, NP, Fan, NB, Wls) was computed for each subject in each group. The same procedure was followed for approach behaviours (FD, LD, AG and Bu).

5.10 (e) Results

Comparisons of the mean duration of total approach and

withdrawal behaviours (Fig. 11) reveals that although the mean duration of withdrawal in group N (nest building) is almost 3 times that of group XN, the difference only approaches significance (Mann-Whitney U, $p>.052$, 1 - tailed). Group XN shows significantly higher durations of agonistic behaviours (Mann-Whitney, $p<.05$). Fig. 12 shows the course of withdrawal for N and XN subjects over successive minutes of testing. Mean duration of withdrawal was initially highest in the N group and declined in both groups. The course of median withdrawal duration is shown if Fig. 13. In neither group was this nonstationarity significant (Friedman: Group N, $p>.20$; group XN, $p>.90$). The number of subjects showing withdrawal behaviours declined in group N from 9 in the first minute of testing to 2 in the 15th minute, while the number of subjects showing withdrawal in group XN declined from 5 in the first minute to 1 in the 15th minute (Fig. 14). Fig. 15 shows the course of mean approach duration over successive 1min. periods of testing. In both N and XN groups the mean number of seconds spent in approach behaviours increased. In group XN, approach duration began at a higher level than in group N and increased more rapidly. The group XN increase was, however, followed by a decrease in mean approach duration after the 5th minute of testing. This was a result of 2 XN subjects showing a decrease in approach during the test. This decrease can be explained by an increase in withdrawal for only one subject. The other became less responsive generally. Median duration of withdrawal showed little decline (Fig. 16). Over the test, only group XN showed a significant increase in approach (Friedman: Group N, $p>.30$; group XN, $p<.001$).

5.10 (f) Discussion

In response to a displaying rival, most nest building males and some males without nests initially showed withdrawal behaviours. Males without nests showed significantly more approach behaviour and nonsignificantly less withdrawal.

Both groups gradually changed their behaviour, increasing approach and decreasing withdrawal. Only in males without nests was the increase in approach significant. The previous experiments showed that subordinate elicited withdrawal was dependent on reproductive factors and morphologically similar to behaviour elicited by a reproductive female. This supports the hypothesis that withdrawal was caused by sexual tendencies. These may predispose the fish to respond to any conspecific with courtship and the conspecific's displaying may gradually inhibit this behaviour. The difference between the behaviour of males with and without nests was not just in the amounts of withdrawal they initially showed to a subordinate, but in the rates at which these declined and agonistic behaviour increased. This could be in part due to a difference observed in the display of stimulus fish. When withdrawing males were several fish-lengths from the stimulus fish, the latter would often not maintain their own frontal display, instead making "following" movements. Only when the subject approached it again would the stimulus fish show further frontal display. Thus, if display in the stimulus inhibits withdrawal, the behaviour of withdrawing may reduce the displays that inhibit it.

5.11 Sexual Discrimination in the Male Betta Splendens

Robertson and Sale (1974) state that,

> "...the rapidity with which the male discriminates the sex of an intruder seems of real advantage for a species as aggressive as Betta splendens."

If sex discrimination is taken to mean not responding to a male with sexual behaviour, then the previous experiments show that when the male stimulus is confined at least, discrimination is far from rapid. If a male is in a reproductive state it will court a conspecific of either sex, only showing continuous aggressive display when the stimulus returns that display.

It is being suggested that the reproductive cycle in

male Bettas determines the fish's predisposition to respond to a conspecific with predominantly courtship or agonistic behaviour. If the resident male is in reproductive condition, then the behaviour of the intruding fish will determine whether or not the resident shifts from predominantly sexual to exclusively agonistic behaviour. The relations between sexual and agonistic motivational systems may therefore be such that if sexual tendencies are at a low level because of the male's position in its reproductive cycle, then all unfamiliar conspecifics will be responded to with aggressive display. Since nest building males responded to subordinate males and reproductive females with similar amounts of courtship and agonistic behaviour, the markings of reproductive females must have little, if any, effect of eliciting courtship or inhibiting threat in reproductive males. Whether the markings of the reproductive female can stimulate courtship in a non-reproductive male to an extent greater than the stimulating effect of the presentation of any conspecific, is a question which has not been answered by the experiments reported here. Until stimulus control of courtship behaviour has been investigated, it can only be said that aggressive display in a conspecific can gradually inhibit courtship behaviour, but it is not clear whether the sexual displays and markings of female conspecifics can inhibit male aggressiveness, where this aggressiveness is associated with that male's reproductive cycle.

At this stage in the discussion, it may be well to point out that the fluctuations in the predisposition to show courtship behaviour occurring over nest building cycles, may not be attributable to causes similar to those controlling the changes from threat to nest-related behaviours in the short term. Even the most highly sexually motivated males approach females with frontal and lateral display and for some time into the courtship bout intersperse their nest-related behaviours with such approaches. Whether these minute to minute transitions in behaviour can be modified by the female's behaviour and markings may require an answer

different from the question of the female's ability to elicit courtship in a non-reproductive male. Miller and Hall (1968) in their investigation of courtship in Trichogaster leeri, do appear to distinguish the factors controlling general sexual readiness and the factors controlling momentary sexual and aggressive behaviour. They state that,

> "Major internal changes, probably associated with endocrine activity, produce a characteristic motivational state that exists throughout a spawning sequence and perhaps for considerable periods before and after spawning..."

and with regard to short term changes that,

> "... cessation in male courtship and increased aggressiveness develop gradually as a result of continued female unresponsiveness".

They further add that,

> "High aggression (male) sequences tend to be those in which female responsiveness (or sexual initiative) is minimal".

In an unconstrained situation, the female may therefore have some control by her behaviour over short-term changes in male aggressiveness.

It was suggested earlier that the test situation may have rendered the sex discrimination mechanisms of the male Bettas studied, less effective than they might have been in a more natural situation. It may be useful to consider both the way in which the sex discrimination mechanism proposed might work effectively in a more natural situation, and the usefulness of the concept of sex discrimination itself, in some detail.

It can be suggested that discrimination of the sex of a conspecific as such may be unnecessary for a species to function. The problem for any animal is not to determine the sex of all conspecifics, but rather to adopt appropriate behaviour towards individual conspecifics who potentially differ in many ways. This is not to say that the sex of

the conspecific may be unrelated to its likely behaviour, in that, for example, a female may never be in competition for territory, but rather to suggest that sex discrimination may be insufficient for the adoption of an appropriate response. In the case of Betta splendens, it may be inappropriate to respond to all females with purely sexual behaviour, since non-reproductive females often destroy nests apparently in search of eggs to consume.

Robertson and Sales'(1974) analysis appears to assume that females are always to be responded to with courtship, whereas it is more likely that the value of discriminating sex as such is relative to the degree that the sex of the intruder predicts its future behaviour (cf. the "Kumpan" hypothesis; von Uexkull, 1934). If other indicators, such as the behaviour of the conspecific (e.g. flight in response to threat), are stronger indicators of that conspecific's future behaviour, then these may be used instead. In the wild type of Betta, where sexual dimorphism is limited and whose native environment may involve relatively poor visibility, behavioural indicators of future behaviour are perhaps more likely to have evolved than a sex discrimination mechanism.

If the nature of the conspecifics likely to be encountered by a territorial male Betta is considered, the 'failure' of sex discrimination in the experiments reported may be easier to understand. Such a male, when freely swimming about its territory, may be approached by a rival male and reproductive or non-reproductive females. Only the latter can safely be allowed to remain in the territory for long. A subordinate male, when approached by the resident in frontal display will give way and slowly move out of the territory, or else remain and begin to display aggressively. Non-reproductive females, when displayed to by the resident, will usually adopt submissive markings and posture similar to the subordinate males and will remove themselves from the territory. If they do display aggressively to the resident,

it is usually very briefly and when the female is large and the male is small. In such a case, mutual display will continue until the female flees. Only reproductive females and rival males will stay in the territory for some time after they have been met by frontal display. The female of these two types of conspecific will not raise the opercula in a frontal display while the rival male will immediately do so. For this reason, a sufficient basis for discrimination exists.

If the territorial male is highly sexually motivated, it may, even in an unrestrained situation, take some time for initial courtship of a rival (the following of brief periods of agonistic display by leading to the nest) to change to continuous agonistic display, but this may not be particularly costly, since the courtship behaviours involve swimming away from the (dangerous) rival and injury is therefore unlikely to result. The change may be speeded up by the rival following the leading resident and maintaining frontal display.

Considering the test situation used in the experiments reported here, it is easy to see how such a mechanism could lead to males courting males. In the natural situation, subordinate males would always flee from a resident which approaches in frontal display. The confinement of the subordinate male prevents this. In addition, where the male stimulus displays, it cannot, because of its confinement, maintain close contact with the resident while the resident is leading to the nest. It has already been mentioned that subject males who began by performing much withdrawal may have been slower to shift to continuous agonistic display because during their lengthy periods away from the stimulus, the stimulus fish attempted to follow at a distance, rather than maintaining frontal display. The test situation may therefore have removed cues important for the adoption of an appropriate response to male conspecifics.

The above is not intended to imply that the differences

found by Robertson and Sale (1974) in the behaviour of males to visually differing conspecifics are not genuine effects, but rather to suggest that they are not the most important factors for the control of male social behaviour, and that they are not the basis of a sex discrimination mechanism in the sense that the term suggests. Evidence exists that the internal state of males of several fish species determines their initial response to a conspecific, and that the behaviour of those conspecifics is the prime factor in the ultimate adoption of appropriate behaviour. Baerends (1971, p. 307) describes male Tilapia mossambica leading other males to the nest when highly sexually motivated. For the same species, Baerends and Baerends van-Roon (1950) state that sex recognition is dependent on the behaviour of the intruder in response to the initial lateral display or butts in the genital region of the resident. The significance of movements for sex recognition has been stressed for Betta splendens by Lissmann (1933).

That behavioural indicators of sex, even when they accompany a high degree of sexual dimorphism, may take some time to be effective is also suggested by the observation in this laboratory that male Guppies (Lebistes reticulatus) when kept together without female will court each other for minutes at a time and that this courtship will involve repeated copulation attempts.

Returning to Betta splendens, the frequency with which sexually motivated behaviour is observed to occur between males, even when the male stimulus displays aggressively, demands that the behaviours reported in the literature as being of an aggressive nature be reexamined. The following section provides alternative explanations of the results of several such experiments in the light of the conclusions reached here about the sexual causation of some inter-male displays.

5.12 (a) Inter-Male Courtship: The Implications for the Interpretation of Studies of Betta Splendens' Aggressive Behaviour

The readiness with which male Bettas show courtship behaviours to male conspecifics in the present test situation demands consideration of the possibility that these may have occurred in other studies of Betta splendens' aggressive display. It is possible that their causation may have been assumed to be aggressive or fearful because of the context in which the observations were made. When two males of a species are placed together, the experimenter's expectations are that the behaviours observed are aggressive in both their causation and function. Even if the experimenter is familiar with Betta sexual displays between male and female, the fact that sexual encounters are usually observed without the confinement of one of the two fish may make identification of sexual behaviour difficult in a test situation where one fish is restrained.

Scrutiny of experimental reports for evidence of the occurrence of intermale sexual behaviour is made relatively easy by the observation, consistent in all the experiments reported here, that when a male (who is not submissive) leaves the site of the conspecific he is displaying to, this withdrawal is always accompanied by the displays Usw and StME. These behaviours and withdrawing itself have been shown to be related to nest building tendencies and to constitute much of the displaying which occurs between reproductive males and females. In addition, withdrawals from subordinate male conspecifics occur much more often in nest-building males than in males who are not nest building, and when they occur to displaying males they usually do so at the beginning of the encounter, and after a few minutes of display, cease to occur. These characteristics of withdrawal and the finding that the frequency of this behaviour is negatively correlated with the behaviours occurring close to a conspecific, indicate that it may be a useful indicator

of the level of occurence of all the behaviours found to be nest-related and which constitute courtship. In surveying the literature on Betta aggressive behaviour in which descriptions of the displays occurring are often insufficiently full to account for a large proportion of the test time, or where the behaviours observed are described in such a way that it is not certain that they are the "same" behaviours as reported by other authors, an observation that the subject repeatedly draws away from the stimulus fish is probably enough to allow a reasonably confident assertion that intermale courtship occurred.

Several reports of experiments involving the presentation of male conspecifics or mirror images in studies of aggressive display and aggression reinforcement may be open to interpretations differing from those advanced by their authors. Rhoad, Kalat and Klopfer (1975) compared the operant performance of male Bettas, reinforced by presentation of their mirror-images; by displaying male conspecifics; by moving models of displaying conspecifics, and similar but stationary models. They found that for all of these reward stimuli, the subjects' aggressive display declined sharply along with their operant response rate. The authors suggest that the decline in display that they observed may be due to habituation or associative learning processes, and this suggestion is supported by their finding that a change in the reward stimulus reinstates both display and operant responding. It may be, however, that the decline in aggressiveness reported is due to, or is accompanied by, an increase in courtship behaviour to the reward stimuli. This is suggested by the author's description of the behaviour accompanying the decline in display as an active avoidance of a stimulus previously sought. This description includes the following statements:

> "... experimental fish could scarcely be said to be ignoring the stimulus..."
>
> "After an initial few attacks, he (the subject) generally assumed a position at the extreme opposite end of the tank, retaining display coloration, but losing all signs of gill cover erection, fin erection, biting and ramming."

The reasons suggested for the occurrence of this behaviour in subjects, while it does not occur in stimulus fish include the observation that the experimental fish, had a greater area for retreat, and this does suggest that withdrawals form the stimulus occurred frequently. Such behaviour would be consistent with that expected if sexual tendencies were operating during the inter-male encounter. That increasing sexual behaviour may result from the habituation of aggression will be considered later. Using a runway situation to investigate the differences between performance for display and food rewards in male Bettas, Hogan (1967) describes the behaviour of subjects which did not spend 100% of their time displaying in the following terms:

> "When not displaying, the fish typically swam up and down the runway and, less frequently, remained still for a few seconds in the runway."

Using mirror images to elicit aggressive display in male Bettas, Baenninger (1966) describes the behaviour of some subjects as follows:

> "In the later observations two fish were observed to swim rapidly away from the mirror whenever they caught sight of their own reflections."

Indeed, Baenninger's finding that Bettas spent more time with their reflections than with live habituated males might indicate that the mirror inhibited courtship. Because it displayed back. Similar observations of mirror-induced retreating are reported by de Bruin (1977). His study used mirror image stimulation to produce aggressive displays in male Bettas, in order to determine the role of telencephalic structures in their behaviour. Since many of the categories of behaviour used by de Bruin are similar to those used in the experiments reported here, comparison with the present studies can be made with more confidence than can comparisons of the present studies with those mentioned above. By their response to

mirror image stimulation, de Bruin (1977, p. 61) identifies post hoc three groups of male Bettas. The three groups a,b and c are described in the following way:

> "Group a: Approach followed by frontal display, a short lateral display, and withdrawal, with more than 80% of the time spent away from the mirror during the entire testing period.
>
> Group b: Approach followed by frontal and lateral display; withdrawal behaviour more than 5%, but less than 80% during the first 4 minutes, gradually decreasing during the test and reaching a level of less than 20% after 10 minutes. Usually there is no withdrawal after T10.
>
> Group c: Approach, followed by frontal and lateral display, and withdrawal behaviour less than 5%."

Fig. 17 shows de Bruin's quantitative description of the three groups in terms of the course of FD, LD and Wi behaviours to a mirror image stimulus for a test period of 16mins. In contrast to the studies reported here, Wi, is the time spent away from the stimulus and the data were presented in terms of the percentage duration spent in the various behaviours for consecutive two-min. time periods. Using the same behaviour categories to describe the course of responding to a mirror image over 5 consecutive days, de Bruin (1977, p. 40-41) found that a decline in frontal and lateral display duration was accompanied by an increase in the duration of withdrawal from the stimulus. He also reports that while away from the mirror, males frequently exhibited nest-related behaviours such as nest building, nest posting and fanning.

De Bruin interprets the occurrence of withdrawal and the differences between post hoc groupings of subjects in the amounts shown, in terms of differing levels of aggressiveness underlying the behaviours Wi, LD and FD. Withdrawal is shown by subjects with very low levels of aggressive motivation, while the displays LD and FD represent progressively higher levels of aggressiveness. The differences between groups are considered to reflect the course of aggressive motivation within test sessions. Group a fish, which show continuously high levels of withdrawal and low

levels of frontal and lateral display, are considered to be males in which aggressive motivation remains low throughout the test. Group c fish, which show high levels of LD and FD and low levels of Wi, are considered to have high levels of aggressive motivation throughout the test, and this level gradually increases. Group b fish are seen as an example of a clear temporal change in aggressive motivation because Wi declines and FD and LD increase markedly. A facilitation or progressive increase in aggressive motivation is thought to occur due to the continued presence of the stimulus.

If the behavioural units employed by de Bruin are closely comparable to those used here, and this seems reasonable on the basis of the very full descriptions he provides, then an alternative interpretation of the behaviour of the 3 groups of Bettas can be advanced, based on the postulation of sexual tendencies as underlying withdrawal. De Bruin's group a, which showed continuous high levels of withdrawal, seems comparable to the subject's behaviours observed in Experiments 2 and 3 of this thesis, in which nest-building males were presented with subordinates. Group c, in which a transition from mainly withdrawal to mainly FD and LD occurs, seems comparable to the behaviour of subjects without nests presented with a rival in Experiment 4. In these fish, FD and LD are high, and Wi was low. Group b behaves as did the majority of both nest- building males and males without nests in Experiment 4 when presented with a displaying male; that is, the fish make a transition from high levels of withdrawal to high levels of FD and LD during the test. Even though de Bruin used mirror image stimulation to elicit display, and not conspecifics as did the experiments reported here, the course of behaviour of the three groups of males can be interpreted in terms of differing initial levels of sexual tendencies. In group c, fish spend most of their time close to the mirror because the level of their sexual tendencies was initially low and

interaction with the mirror image would act to lower them even further. De Bruin does not report whether these males had nests or not. Males of group a, who spent most of their time withdrawn from the mirror may have had high levels of sexual motivation before testing. This would result in their approaching the mirror image for very brief periods, and these approaches may have been of insufficient duration for them to have had an inhibiting effect on withdrawal tendencies. The mirror image will of course display to the subject only when the subject is displaying, and according to de Bruin's classification, this would be for less than 20% of the test period. The question which now arises is why males of group b make the transition from much withdrawal to much display during tests. The answer to this may be that this group, according to the basis of classification employed, spent less than 80% of its time away from the mirror during the first 4mins. of sessions. The differences between groups a and b may then be due to a small difference in the levels of their sexual tendencies at the start of the testing such that group b spent just enough time by the mirror for their own reflected display to have an inhibiting effect on their sexual responsiveness and a motivating effect on agonistic display. There may then be a critical duration of aggressive display in a subject, below which that display does not increase its duration in response to its mirror image. The mirror image in such a case, may have much the same effect as a non-displaying conspecific in that for most of the session it does not display aggressively. In Experiment 4 of this thesis, some males with nest showed no transition from courtship to fully agonistic display and it was suggested that because of their high initial levels of withdrawal, the stimulus fish may not have maintained display, particularly FD, during these withdrawal periods and thus did not produce a transition from courtship to aggression. The case of mirror image stimulation could be similar when the subject is highly sexually motivated.

The work of Bols (1977) has been discussed in detail earlier (ch. 3.1(b)), and the suggestion has already been made that the behaviour she describes as elicited by non-displaying males was sexually motivated. As well as the experiment discussed, which used non-displaying males as reward stimuli, Bols (1976) reports an experiment in which the runway performance of male Bettas for a mirror image, for food and for nothing was compared. Fish swam faster for the food and the mirror image than they did for nothing, and faster for food than for the mirror. However, Bols points out that the food-mirror difference is due to the mirror group remaining motionless for longer periods of time during trials, and turning away from the goal box more frequently. This turning back is considered a direct measure of avoidance by Hogan and Roper (1978, p. 205) and they suggest that asymptotic level of instrumental responding for different reward stimuli as found by, for example, Thompson (1963) and Rhoad et al. (1975) may reflect differences not just in aggressive motivation but in escape motivation also. For this reason they state that,

> "Asymptotic rate of responding is a measure of attack less escape motivation..."
>
> (Hogan and Roper, 1978, p. 205)

Although such processes as escape and attack may be involved in jointly determining the reinforcing strengths of an aggression eliciting stimulus (and it is premature to consider the relation an additive one) the implication of sexual tendencies in the motivation of some withdrawal behaviours at least, means that the identification of any movement away from the stimulus and "avoidance" is questionable.

The basis for invoking escape tendencies in the explanation of reward elicited behaviour that is, the observation of escape-like movements, seems to have been removed by the demonstration that their occurrence can be accounted for by sexual tendencies alone. Indeed only two experiments remain to implicate fear directly in the control

of operant behaviour for aggression reward. Using a runway situation allowing male Bettas the choice between food and their mirror image, Hogan (1974) showed that fish preferred food when they lived permanently in the test apparatus, but preference shifted to their mirror image when fish were transferred from their home tanks to the runway just before testing. Fantino, Weigele and Lancy (1972) also found a preference for mirror image over food when male Bettas were transferred to the operant situation (ring swimming operant) just before testing. It seems that fear, if that is the state induced by transfer from the home tanks, can reduce operant performance for food more than it does performance for an aggression eliciting reward. This suggests that a mirror image stimulus, or the display it evokes, may be more effective at inhibiting the effects of fear than is the consumption of food. This still leaves the question of the degree to which fear determines operant performance when that fear is evoked by the reward stimulus itself. To answer this, comparisons of operant performance for sizes of reinforcer conspecific might be useful, since it could fairly safely be assumed that larger opponents would elicit more fear than smaller ones. The occurrence of overt withdrawal responses however can no longer be considered a sufficient basis for the statement that escape tendencies are present, because of the role of sexual tendencies in their motivation.

It was suggested earlier that habituation of aggressive behaviour may result in the occurrence of sexual behaviour to the habituating stimulus. It has been reported for both Betta splendens and the 3-spined stickleback (Gasterosteus aculeatus) that when aggressive behaviour is reduced by an experimental treatment, sexual behaviour increases.

Peeke (1969) habituated agonistic behaviour in male sticklbacks by repeatedly presenting them with a male conspecific. While agonistic behaviour waned, a concomitant increase in sexual behaviour (frequency of zig-zags) towards

the stimulus male was observed to occur. In Betta splendens, Klein, Figler and Peeke (1976) found that the habituation of aggressive behaviour was often accompanied by inter-male sexual behaviour, being unmistakeable in that it included variants of the spawning ~~clasp~~ clasp. That this phenomenon may not be a result of habituation per se, but of any reduction in aggressive tendencies, is suggested by the findings of Figler, Klein and Radford (1973) with male Betta splendens. In these studies, aggressive behaivour was reduced pharmacologically by treatment with chlordiazepoxide and clear variants of the spawning clasp were again observed to occur between males. These results taken together with the findings of the experiments reported here lends considerable support to the view of the relationship between sexual and aggressive tendencies taken by Sevenster (1961, p. 146). To explain the occurrence of displacement activities he states that,

> "...sex and aggression form a system of mutual inhibition, with a given absolute level of the sexual drive, its relative level is determined by the absolute level of of the aggressive drive and vice versa".

The usefulness of this theoretical formulation is however limited by the conception of the relevant drives in unitary terms. This may not be appropriate, since the results of Experiment 2 of this thesis suggest that agonistic display and overt aggression (biting) may be to a large extent independent. Supporting this suggestion is the factor analysis study of Robertson and Sale (1974) which showed that at least 3 separate factors were needed to account for Betta aggressive sexual displays. Apart from these reservations about the unitary nature of the sex and aggression systems themselves, the relations between these systems or at least some of their subsystems, do seem to be inhibitory.

5.12 (b) Sexual Behaviour and Its Control For Aggression Reinforcement Experiments

Turning to the matter of designing aggression reinforcement

experiments with male Betta splendens, it seems desirable that the effects of sexual tendencies on reward-elicited display in operant experiments should be minimized. This is not to say that the interactions between sex and aggression systems or their combined effects on operant performance are not of interest, but only to suggest that at an early stage of investigation of the determinants of operant performance, the situation should be kept as simple and as replicable as possible. Neither is it suggested that sexual tendencies can be completely eliminated from subjects for the purposes of such experiments. All that can be achieved is to minimize the behavioural effects of such tendencies, thus reducing inter-subject variability.

From the results of the experiment reported earlier, it might seem that the easiest way to reduce the influence of sexual tendencies on reward elicited behaviour would be to select subjects which are not in nest building condition. However, because the course of nest building is cyclical and because the presentation of any conspecific can stimulate nest building, it would be difficult to complete an operant experiment taking several days to execute, without subjects coming into reproductive condition at least once. However, both nest building males and males who have not built nests will shift from initial courtship (if any is shown) to continuous agonistic display if they are presented with a displaying conspecific, and if they are allowed some time in which to make the transition. Once withdrawal behaviours have not occurred for a period of about 30secs., they seem unlikely to occur during the rest of the session. Furthermore, once a subject has made the transition from courtship to continuous agonistic behaviour, its display cannot be distinguished qualitatively from that of a subject which showed full agonistic behaviour right from the start of the test. A method for reducing the effects of sexual tendencies on reward elicited display might then be to precede each operant session with non-contingent presentation

of the reward stimulus, lasting until no withdrawals have occurred for, say, 30secs.. All subjects would begin the session with an approximately equal and very low probability of withdrawal, even though this probability might have been brought about by different amounts of preexposure. In addition, pilot studies revealed that some stimulus males are themselves reproductively motivated,and thus predisposed to respond to the subject not with agonistic display but with vigorous thrashing movements inside its container. These movements resemble fright, but display coloration is maintained, and if the fish is released from its container, it will perform undulating swimming and stop with its medial fin erect. The thrashing observed probably represents attempts by the stimulus fish to lead the subject to its (non-existent) nest. This behaviour in the stimulus can be prevented, and its agonistic display between "visits" of the subject maximised, by preexposing the stimulus fish to a third male for a brief period of time. By these means, it can be assured that both subject and stimulus males respond appropriately (i.e. agonistically) when the subject is reinforced for an operant response. All the following experiments with Betta splendens utilize this method.

Figure 3

The mean durations of behaviours in the first session of subordinate (S) and rival (R) conditions. Bars equal one standard error.

Significance testing by Wilcoxon matched pairs test (2-tailed).

	LD	FD	AG	Bu	Usw	StME	Wls
T =	8	4	4	7	1	0	0
N =	7	7	7	7	7	7	7
P =	N.S.	N.S.	N.S.	N.S.	$<.05$	$<.02$	$<.02$

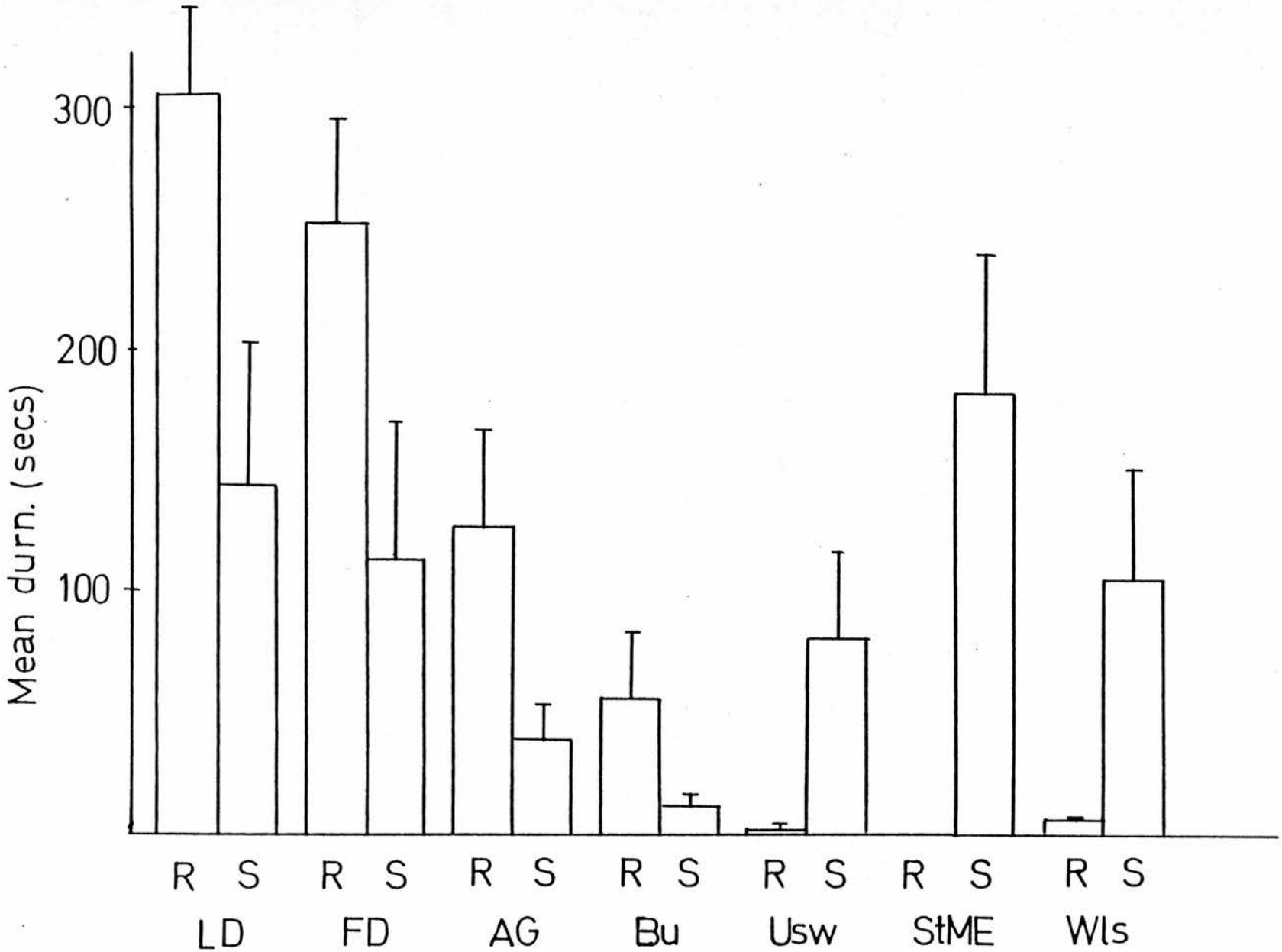

Mean durn. (secs)
300
200
100
R S R S R S R S R S R S R S
LD FD AG Bu Usw StME Wls

Figure 4

The mean frequencies of behaviours in the first session of subordinate (S) and rival (R) conditions. Bars equal one standard error.

Significance testing by Wilcoxon matched pairs test (2-tailed).

	LD	FD	AG	Bu	Bi	TB
T =	4	6	1	5	1	0
N =	7	7	7	7	7	7
P =	N.S.	N.S.	<.05	N.S.	<.02	<.02

	Wi	Usw	StME	Wls
T =	0	1	0	0
N =	7	7	7	6
P =	<.02	<.05	<.02	<.05

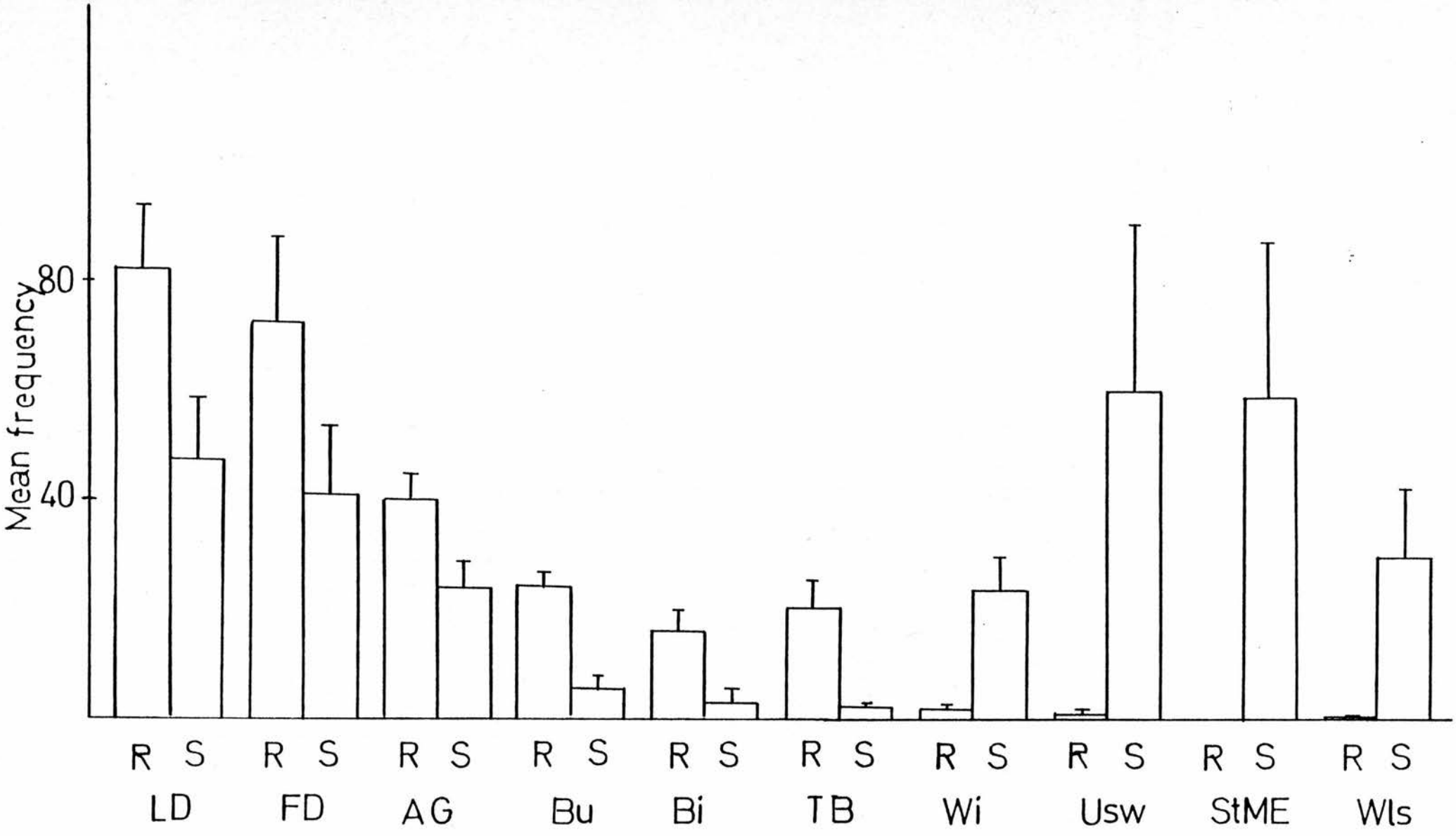
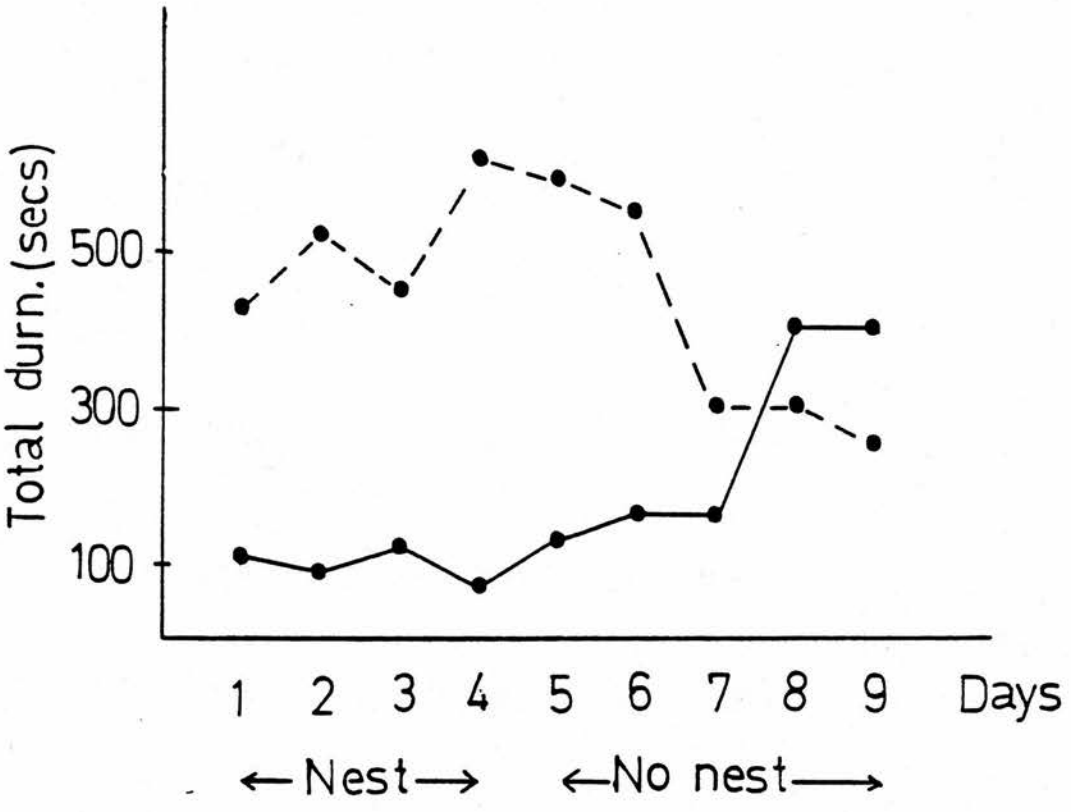

Mean frequency
80
40
R S
LD
FD
AG
Bu
Bi
TB
Wi
Usw
StME
Wls

Figure 5

Behaviour of a single subject to a subordinate over days.

_____ represents total duration of FD, LD and Bu.

_ _ _ _ _ represents total duration of Usw, StME and Wls.


Total durn. (secs)
500
300
100
1
2
3
4
5
6
7
8
9
Days
← Nest →
← No nest →

Figures 6 - 8

The mean frequencies of behaviours to a subordinate in the nest (N) and no-nest (XN) groups. Bars represent one standard error.

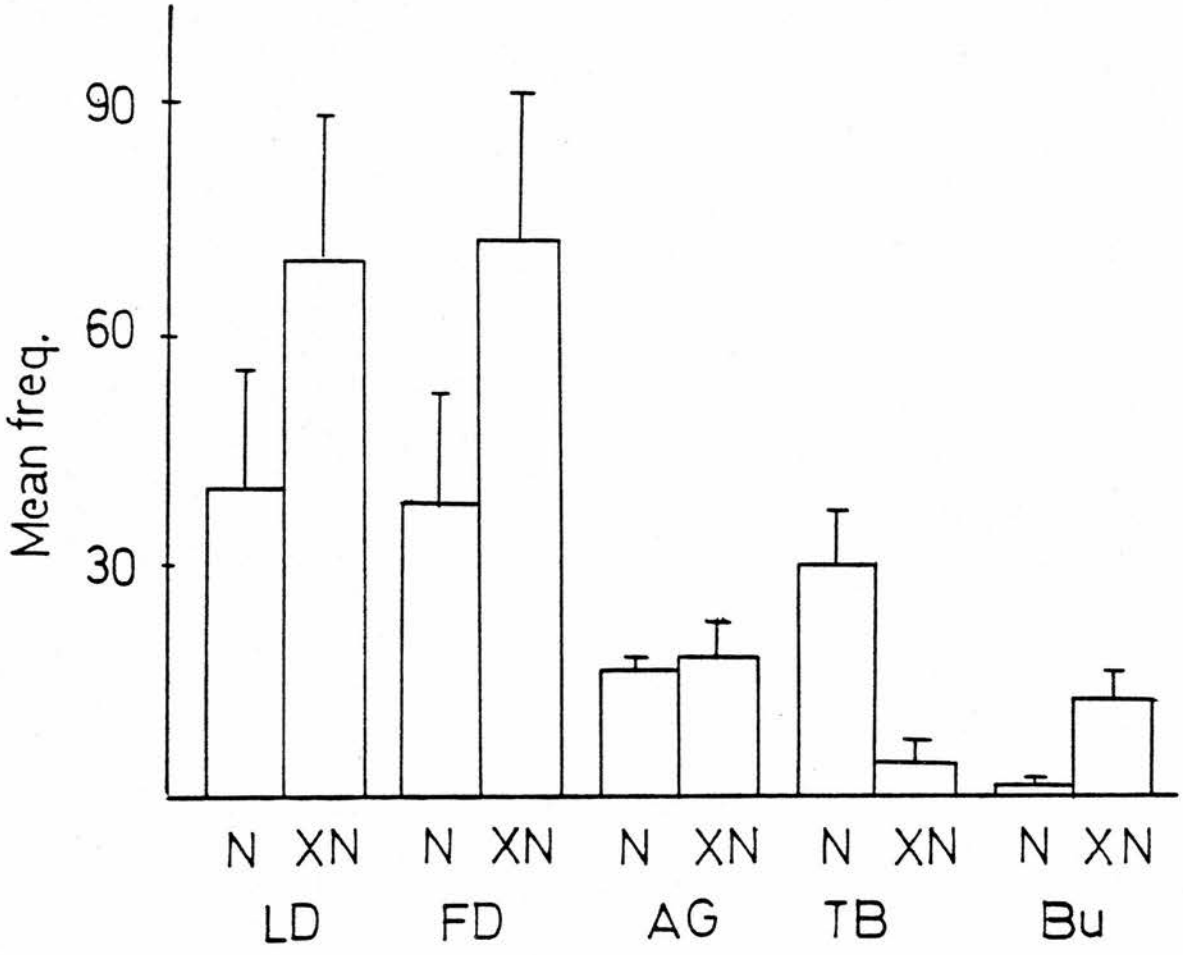
Significance testing by Mann-Whitney U test (1-tailed).

* denotes 2-tailed significance when the difference was not in the predicted direction.

N = 7 for each group.

		LD	FD	AG	TB	Bu
Fig. 6	U =	13	12	23	2	11
	p	N.S.	N.S.	N.S.	<.002*	<.05

		Wi	Usw	StME	Wls
Fig. 7	U =	2	0	0	2
	p	<.001	<.001	<.001	<.001


90
60
30
Mean freq.
N XN N XN N XN N XN N XN
LD FD AG TB Bu

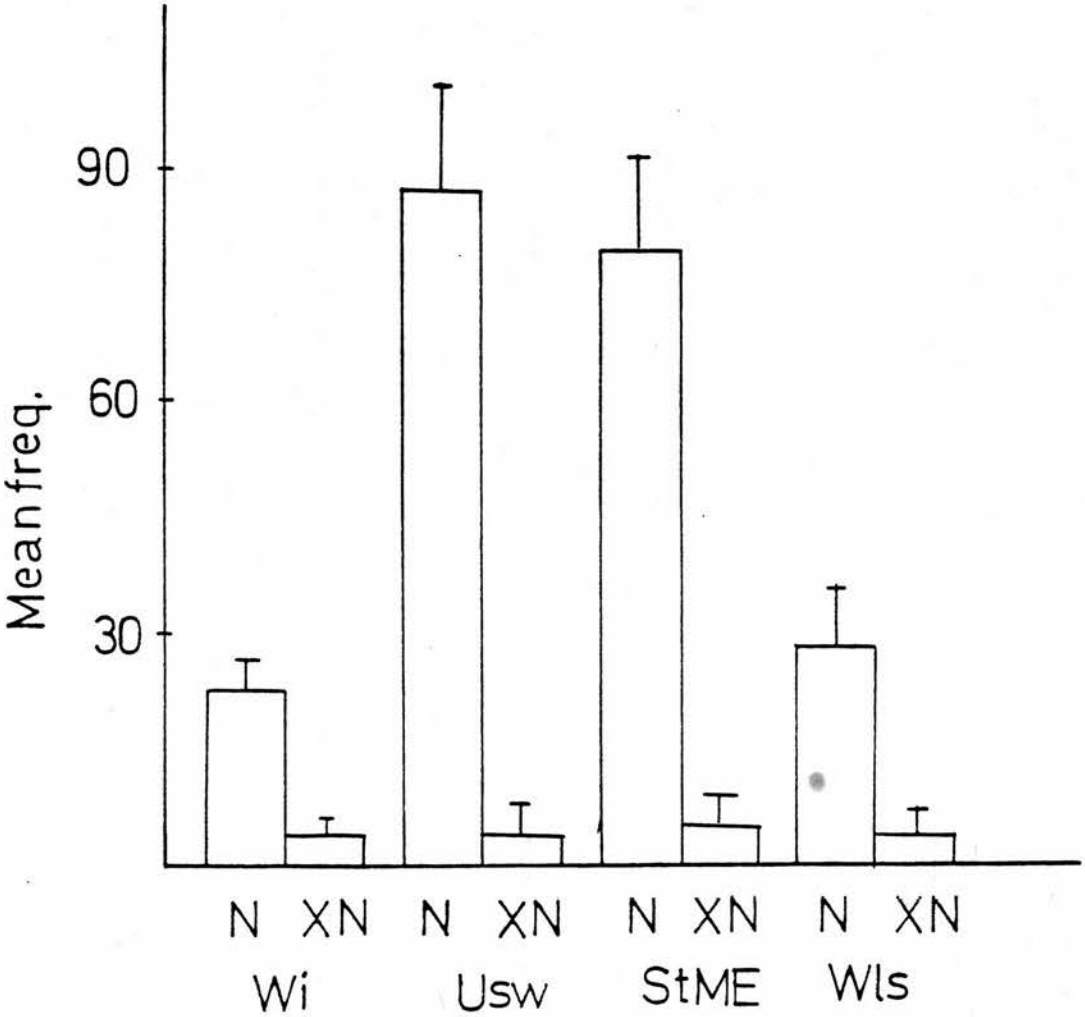
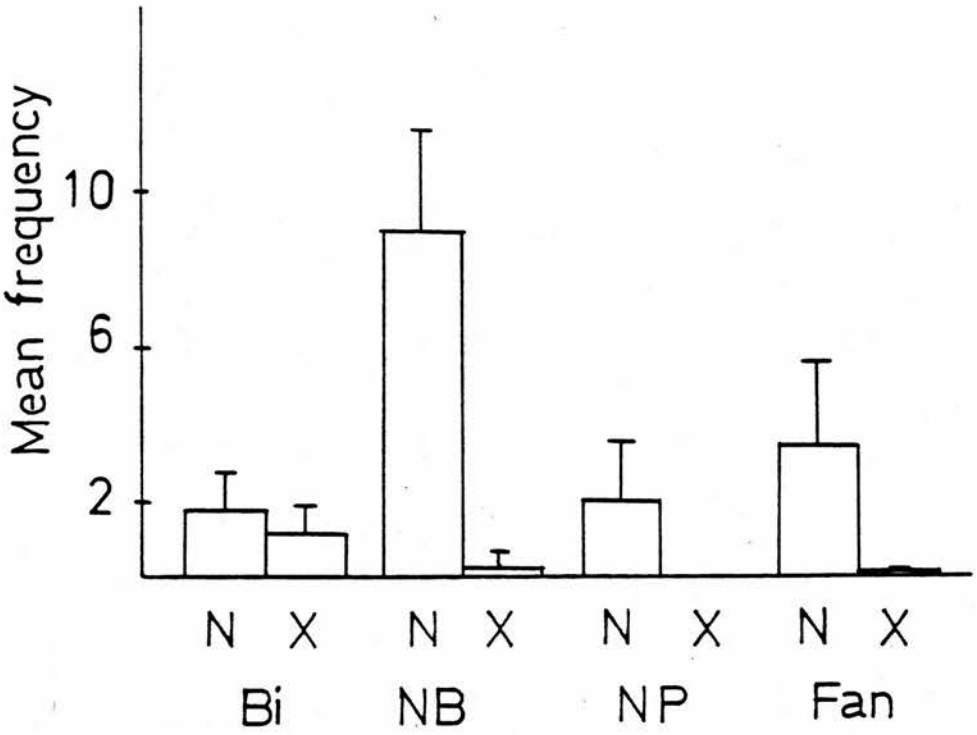

90
60
30
Mean freq.
N XN N XN N XN N XN
Wi Usw StME Wls

Fig. 8	Bi	NB	NP	Fan
U =	18	1	7	10
P =	N.S.	$< .001$	$< .05$	$< .05$


Mean frequency
10
6
2
N X N X N X N X
Bi NB NP Fan

Figures 9 - 10

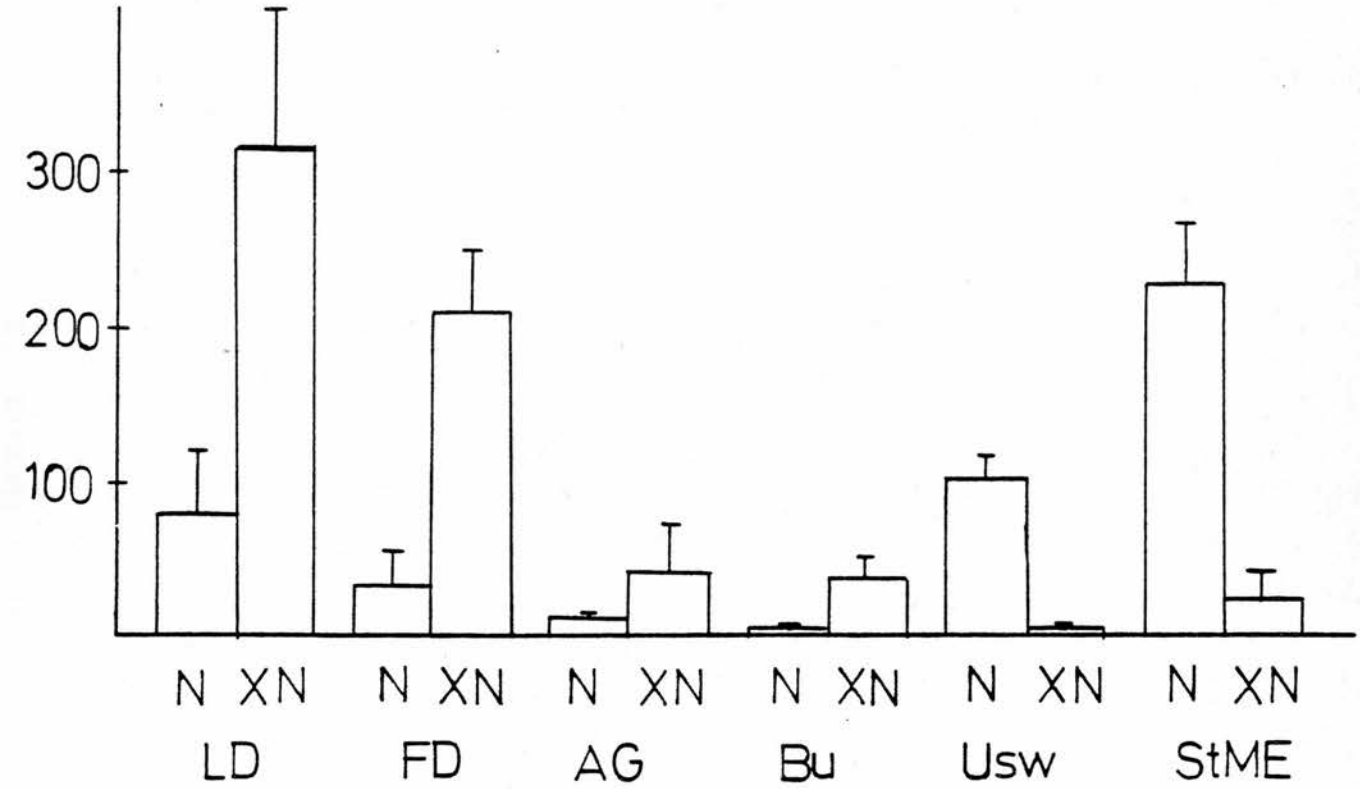
The mean durations of behaviours to a subordinate in the nest (N) and no-nest (XN) groups. Bars represent one standard error.

Significance testing was by Mann-Whitney U test (1-tailed).

N = 7 for each group.

Fig. 9	LD	FD	AG	Bu	Usw	StME
u =	9	3	24	11	0	2
p	$<.05$	$<.02$	N.S.	$<.05$	$<.001$	$<.001$

Fig. 10	W ls	NB	NP	Fan
u =	6	1	7	10
p	$<.001$	$<.001$	$<.05$	$<.05$


300
200
100
N XN N XN N XN N XN N XN N XN
LD FD AG Bu Usw StME

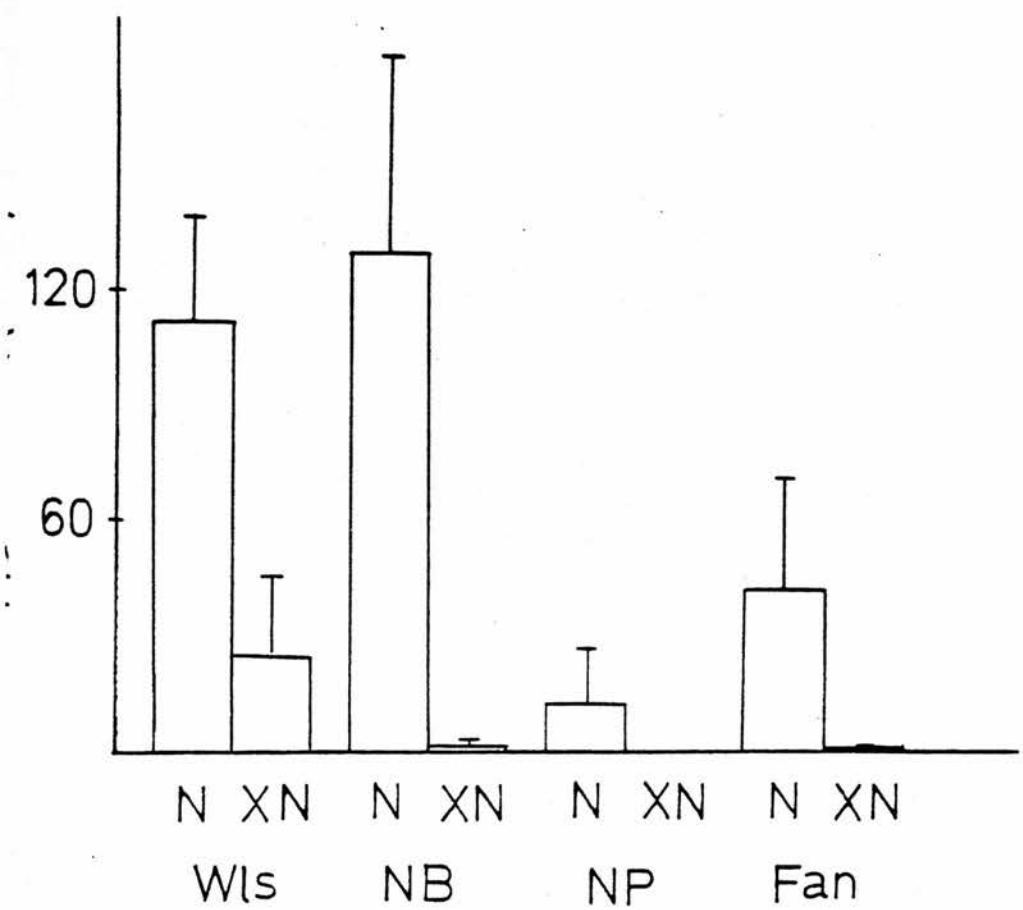

120
60
N XN N XN N XN N XN
Wls NB NP Fan

Figure 11

The total durations of approach and withdrawal in males with nests (N) and without nests (XN) when presented with a displaying male. N = 8 for each group.

Significance testing was by Mann-Whitney U test (1-tailed).

	Approach		Withdrawal	
	N	XN	N	XN
$\bar{x}$ secs.	480.2	733.2	200.3	69.3
SEM	139.7	81.6	87.2	53
U, U'	15,	49	16.5,	47.5
p	$< .05$		N.S.	

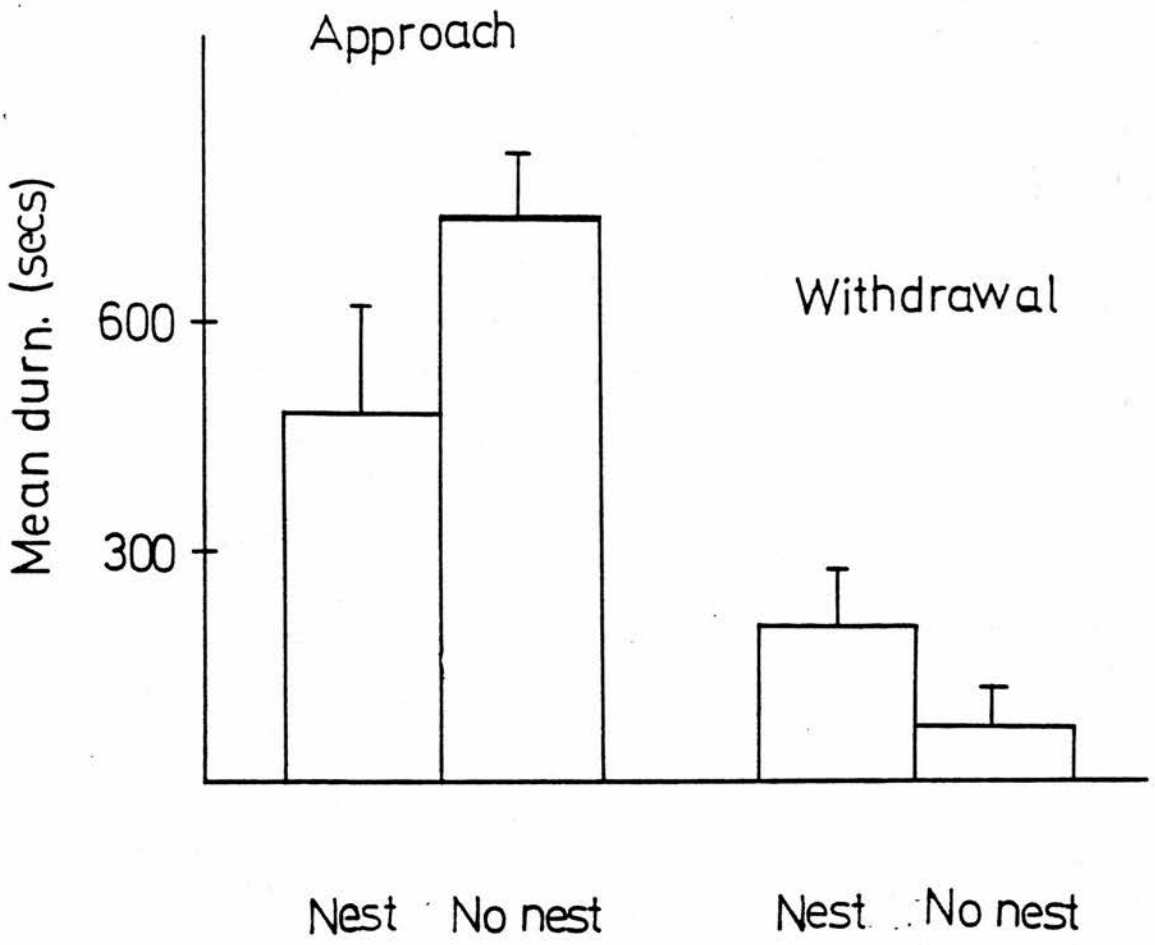

Approach
Withdrawal
Mean durn. (secs)
600
300
Nest
No nest
Nest
No nest

Figure 12

The course of mean withdrawal duration (secs.) elicited by a rival over successive minutes of the test in nest (N) and no nest (XN) groups.

Significance testing by Friedman 2-way analysis of variance.

N = 8 for each group.

N

Mins	1	2	3	4	5	6	7	8
$\bar{X}$ (secs)	15.4	16.1	22.0	17.6	17.0	9.7	12.2	7.8
SEM(secs)	4.5	6.4	8.2	8.0	7.3	6.8	8.6	6.0
Total Ranks	83	79.5	92.5	78	66	54.5	60.5	50.5

Mins	9	10	11	12	13	14	15
$\bar{X}$ (secs)	11.9	13.1	15.1	13.8	11.9	8.3	8.6
SEM(secs)	8.4	8.2	8.3	6.9	7.0	6.3	6.2
Total Ranks	55.0	61	69.5	59	58	48	45

Chi = 16.8530 df = 14 p>.20 , $\omega = .15047$

$L = 8365.5$, $p < .001$

XN

Mins	1	2	3	4	5	6	7	8
$\bar{X}$ (secs)	8.2	8.0	2.4	4.1	2.2	5.2	6.2	6.8
SEM(secs)	4.4	4.2	1.7	3.9	2.4	5.6	6.1	5.4
Total Ranks	80.5	82	56.5	61.5	51	61	70.5	69.5

Mins	9	10	11	12	13	14	15
$\bar{X}$ (secs)	3.6	3.7	4.4	5.0	4.6	5.1	0.1
SEM(secs)	3.6	3.8	4.5	4.8	4.8	5.4	0.1
Total Ranks	68.5	60.5	61.5	67.5	61.5	60	48

Chi = 7.7406 df = 14 p>.90 , $\omega = .06911$

$L = 7962$, $p > .05$

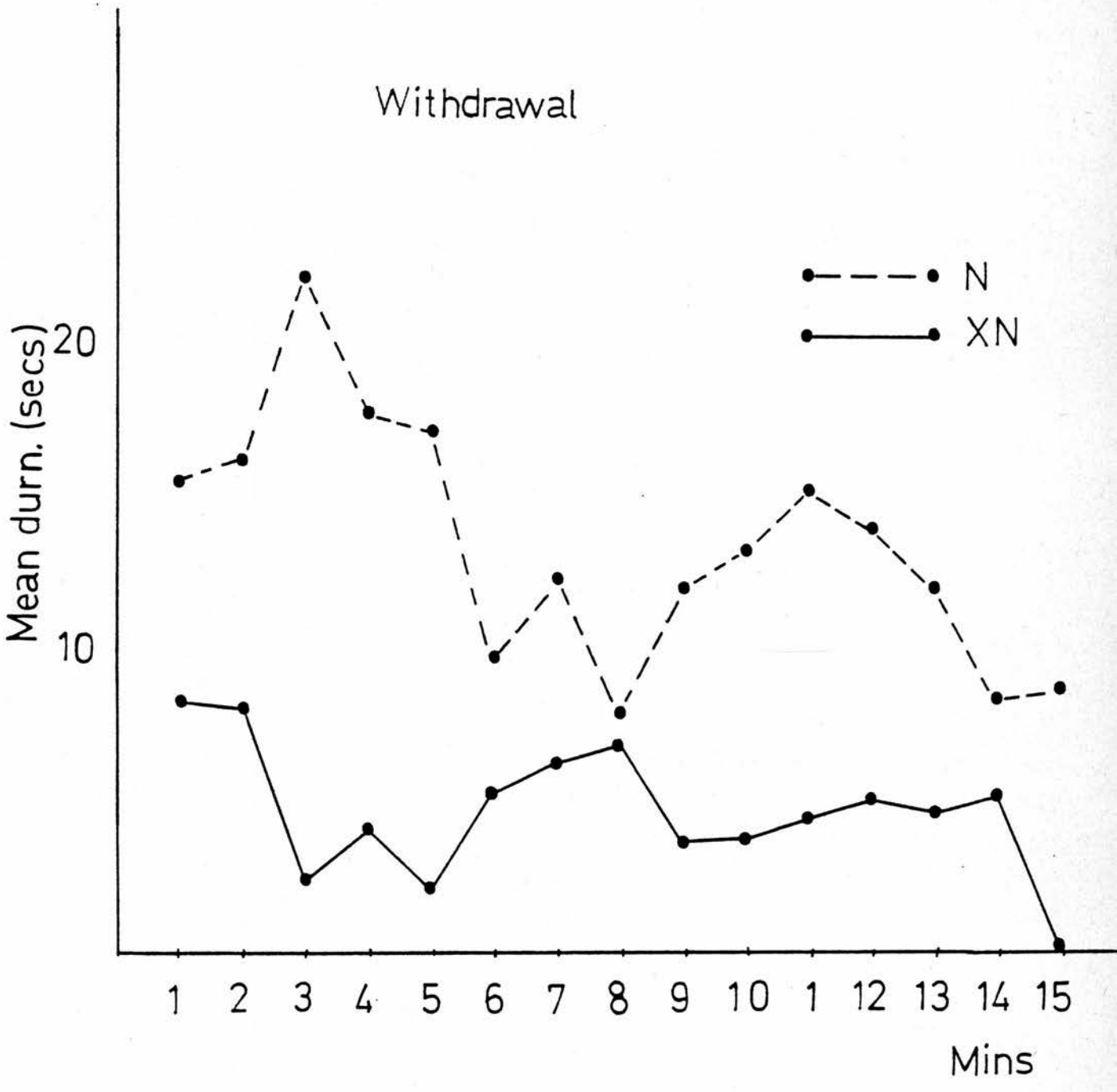

Withdrawal
N
XN
Mean durn. (secs)
20
10
1 2 3 4 5 6 7 8 9 10 1 12 13 14 15
Mins

Figure 13

The course of median withdrawal duration (secs.) elicited by a rival over successive minutes of the test in nest (N) and no nest (XN) groups. N = 8 for each group.

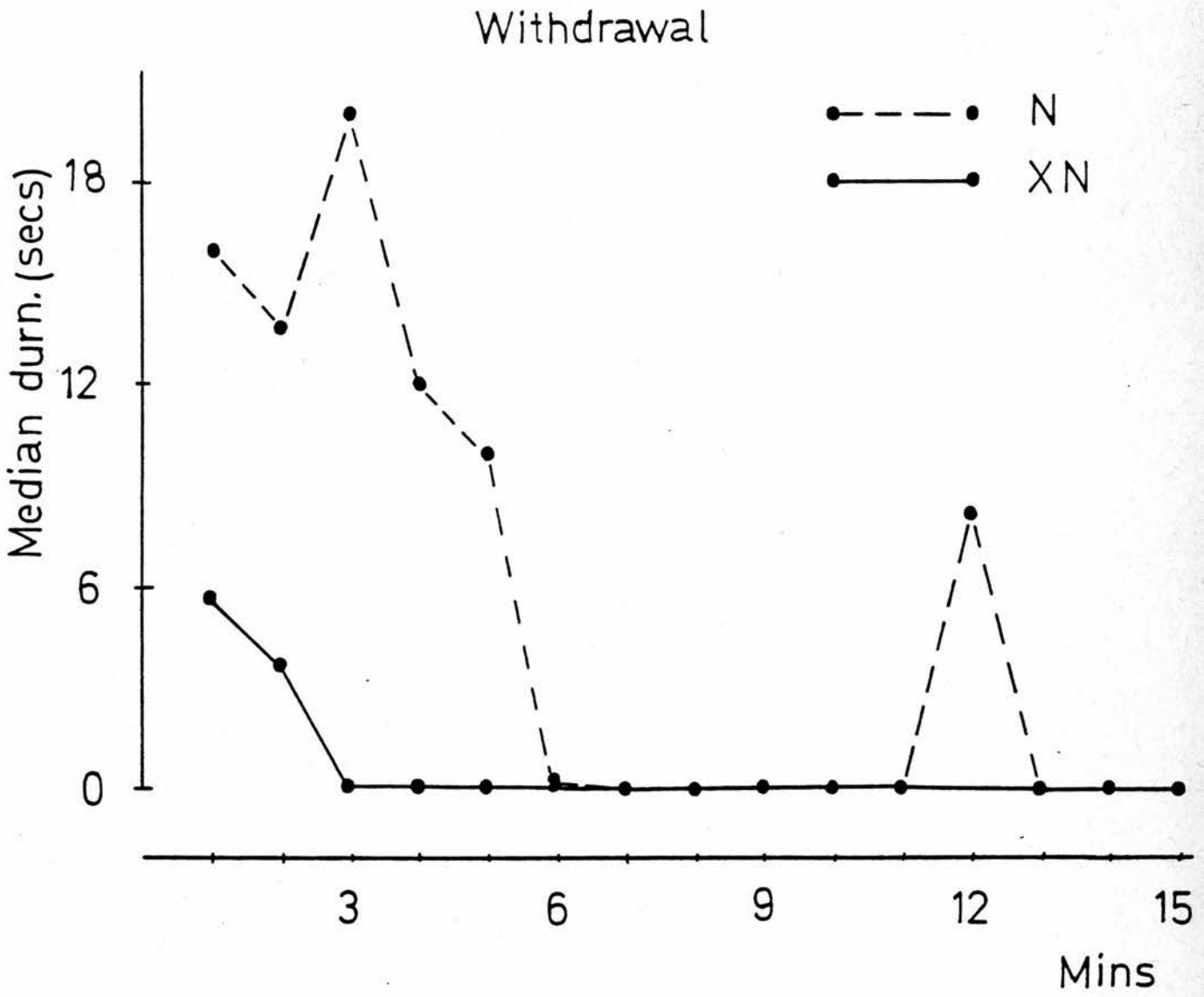

Withdrawal
N
XN
Median durn. (secs)
18
12
6
0
3
6
9
12
15
Mins

Figure 14

The number of subjects in the nest (N) and no nest (XN) groups, showing any withdrawal in each minute of the test.

N = 8 for each group.


Withdrawal
N
XN
No. of subjects
8
6
4
2
3
6
9
12
15
Mins

Figure 15

The course of mean approach duration (secs.) elicited by a rival over successive minutes of the test in nest (N) and no nest (XN) groups. Significance testing by Friedman 2-way analysis of variance.

N = 8 for each group.

N

Mins	1	2	3	4	5	6	7	8
$\bar{X}$(secs)	27.6	26.2	29.5	30.0	30.9	29.7	38.0	35.9
SEM(secs)	6.8	10.2	11.1	11.4	11.2	11.4	10.7	11.0
Total Ranks	48	49	63	78	71	75.5	86.5	74.5

Mins	9	10	11	12	13	14	15
$\bar{X}$(secs)	34.7	36.1	34.5	31.2	29.8	33.3	33.8
SEM(secs)	10.9	10.0	10.7	9.3	9.6	10.4	10.3
Total Ranks	52.5	78.5	51.5	64	45	59	64

Chi = 14·7531 df=14 $p > .30$, $w = .13172$

$L = 7619.5$, $p > .05$

XN

Mins	1	2	3	4	5	6	7	8
$\bar{X}$(secs)	39.1	46.1	55.0	55.5	56.2	53.2	54.6	48.8
SEM(secs)	6.8	5.8	3.6	4.5	4.3	7.7	5.1	7.7
Total Ranks	33	46.5	81	90.5	104.5	90	77.5	64.5

Mins	9	10	11	12	13	14	15
$\bar{X}$(secs)	49.3	47.2	48.8	46.6	46.3	43.3	43.5
SEM(secs)	7.2	8.5	6.0	7.3	7.4	9.6	9.7
Total Ranks	75	59	57	53.5	45	38.5	44.5

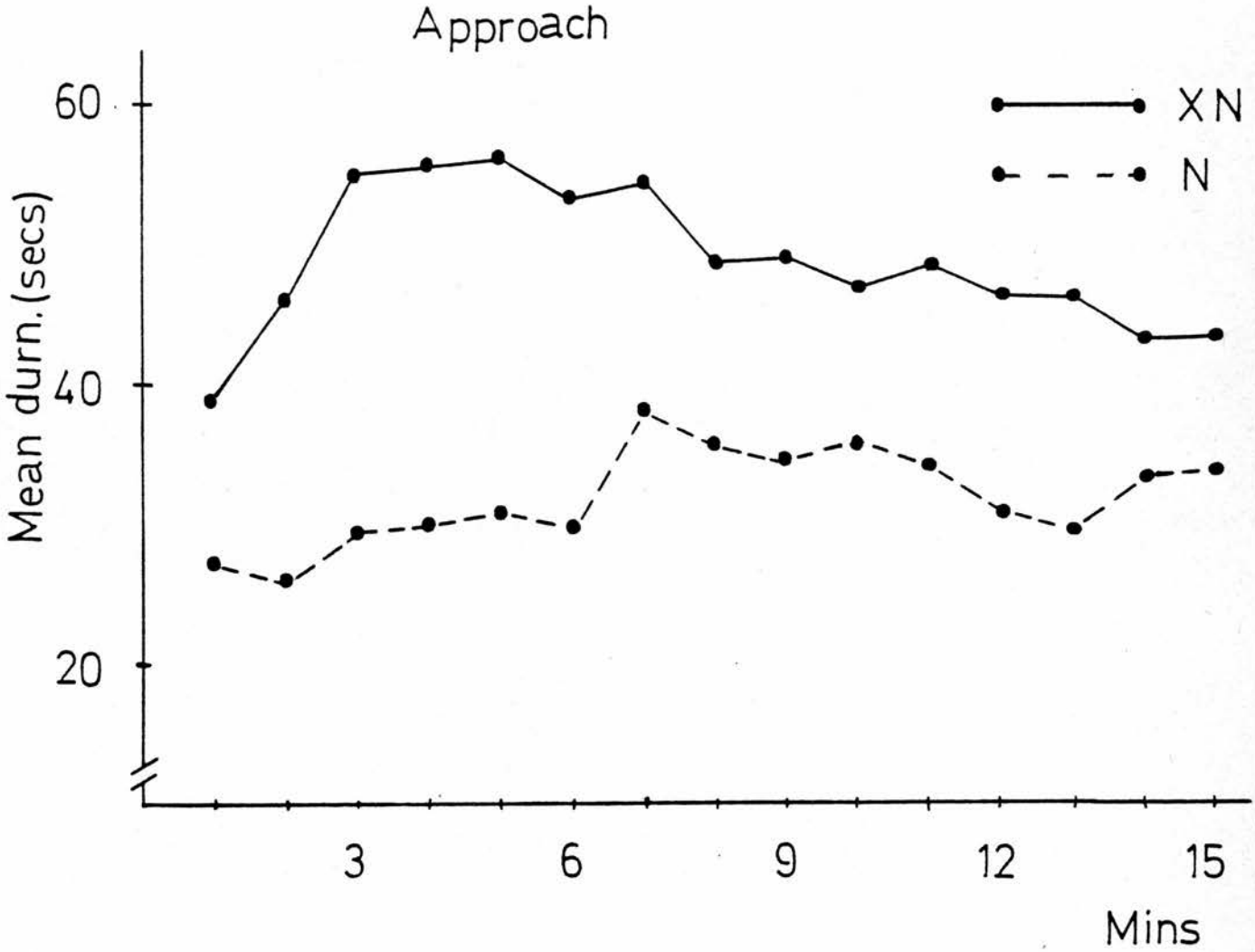
chi = 40·3374 df=14 $p < .001$, $w = .36016$

$L = 7177.5$, $p > .05$

*

Figure 16

The course of median approach duration (secs.) elicited by a rival over successive minutes of the test in nest (N) and no nest (XN) groups. N = 8 for each group.


Approach
60
40
20
Mean durn. (secs)
XN
N
3
6
9
12
15
Mins

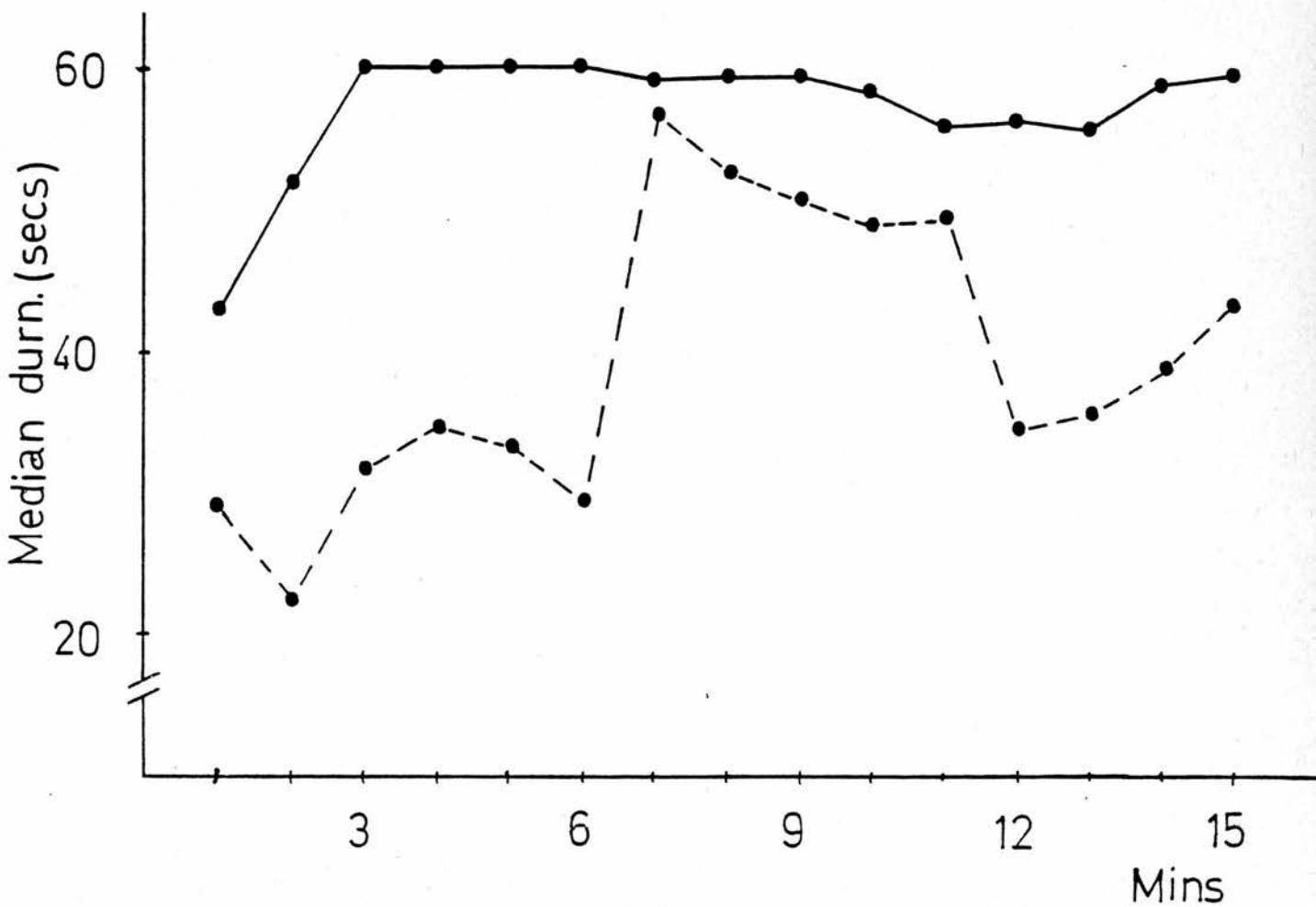

60
40
20
Median durn. (secs)
3
6
9
12
15
Mins

Figure 17

The percentage duration of successive minutes of tests spent in frontal display (FD), lateral display (LD) and withdrawal (Wi), for 3 post hoc groupings (a,b, and c) of male Bettas. From de Bruin (1977,p.65).

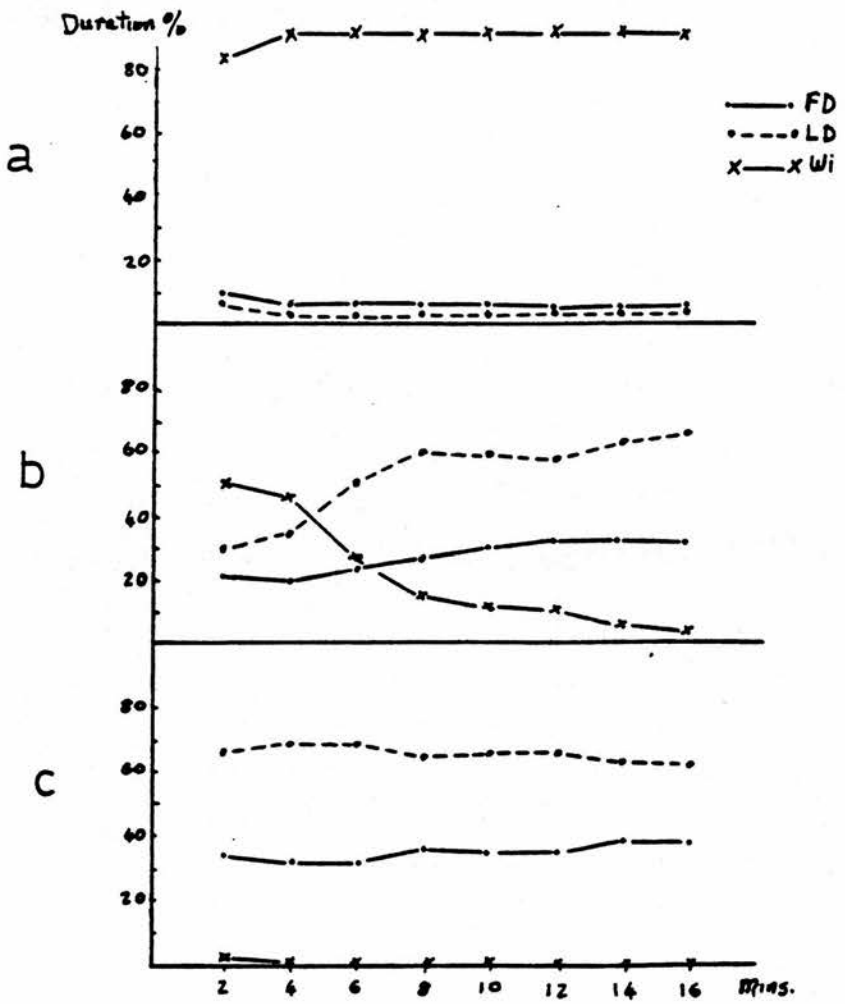

Duration %
a
b
c
80
60
40
20
FD
LD
Wi
2
4
6
8
10
12
14
16
Mins.

Table 1

The durations of behaviours to a subordinate (S) and rival (R) in individual subjects.

Subj.	FD		LD		Usw		(secs.)
	R	S	R	S	R	S	
50	241.2	211	232.0	369.2	9.6	35.6	
82	246.2	284.8	312.6	314.0	2.8	2.2	
46	215	114.2	347.4	159.6	0	49.2	
49	212.8	26.2	240.6	65.6	0	63.2	
36	88.2	23	462.6	46	0	51.8	
53	397.2	3.4	355.0	6.0	0	117.4	
66	376.2	22.6	195.0	54.2	0	254.2	

Subj.	StME		Wls		(secs.)
	R	S	R	S	
50	0	2.4	0	22.6	
82	0	10.4	1.8	4.8	
46	0	239.8	0	95.2	
49	0	339.8	0	27.0	
36	0	117.8	0	55.0	
53	0	344.2	0	310.2	
66	0	225.0	0	214.8	

Table 2

The Spearman correlations between subordinate elicited behaviours. N = 8. Suffix 'f' indicates frequency, suffix 'd' indicates duration.

Significance testing was 1-tailed except for correlations with AG(f).

$p < .05$ indicated by _ _ _ _ _

$p < .01$ indicated by _____

	FD(d)	FD(f)	LD(d)	LD(f)	Bu(d)	Bu(f)	Bi	TB
FD(d)	1.000							
FD(f)	.833	1.000						
LD(d)	.905	.929	1.000					
LD(f)	.786	.952	.929	1.000				
Bu(d)	.755	.347	.707	.395	1.000			
Bu(f)	.826	.491	.707	.515	.976	1.000		
Bi	.381	.304	.583	.381	.510	.485	1.000	
TB	.444	.102	.381	.178	.638	.498	.547	1.000
AG(d)	.191	.143	.381	.167	.287	.264	.799	.495
AG(f)	-.357	-.286	-.119	-.238	-.084	-.132	.406	-.216
Wi	-.551	-.395	-.395	-.299	-.494	-.602	.109	.013
Usw(d)	-.952	-.786	-.810	-.667	-.659	-.755	-.241	-.304
Usw(f)	-.898	-.767	-.767	-.647	-.554	-.663	-.236	-.198
StME(d)	-.714	-.881	-.762	-.833	-.132	-.257	-.152	-.089
StME(f)	-.809	-.667	-.714	-.595	-.479	-.527	-.317	-.457
Wls(d)	-.905	-.762	-.857	-.762	-.671	-.743	-.507	-.368
Wls(f)	-.910	-.719	-.850	-.695	-.753	-.825	-.542	-.402

	AG(d)	AG(f)	Wi	Usw(d)	Usw(f)	StMEd	StMEf	Wlsd	Wlsf
AG(d)	1.000								
AG(f)	.738	1.000							
Wi	-.132	.000	1.000						
Usw(d)	-.191	.333	.707	1.000					
Usw(f)	-.216	.371	.669	.970	1.000				
StME(d)	-.143	.357	.311	.714	.779	1.000			
StME(f)	-.429	.167	.527	.857	.898	.809	1.000		
Wls(d)	-.333	.333	.443	.857	.898	.762	.857	1.000	
Wls(f)	-.443	.179	.590	.898	.916	.671	.862	.970	1.000

Table 3 (3 pages)

The amounts of behaviours to a rival over daily sessions for those subjects which did not produce submission before the second session.

Total behaviour durations (secs.)

(a)

S	1	2	3	4	5	6	7	8	9
50	767.6	826.6	829.2	789.2	832.8	869.8			
49	514.4	563.6	708.4	646.8	689.2	711.2			
53	890	830.2							
36	749	779	714.6	768.4	825.8	782	690.2	788.6	789.6
66	779	808.2	883	730.4					

LD duration

(b)

S	1	2	3	4	5	6	7	8	9
50	232.0	402.0	404.2	461.4	475.2	547.6			
49	240.6	146.4	236.2	254.8	281.2	270.2			
53	355.0	308.4							
36	462.6	413.8	236.8	278.2	464.6	328.6	259.4	381.2	362.2
66	195.0	216.6	215.4	245.2					

LD frequency

(c)

S	1	2	3	4	5	6	7	8	9
50	54	98	86	84	83	84			
49	86	100	93	95	100	99			
53	116	113							
36	80	97	54	96	91	88	69	72	84
66	114	96	95	128					

Table 3 continued

(d) FD frequency

S	1	2	3	4	5	6	7	8	9
50	45	68	57	37	39	40			
49	67	53	48	36	50	36			
53	97	94							
36	46	37	31	35	62	78	50	51	54
66	138	141	133	141					

(e) FD duration

S	1	2	3	4	5	6	7	8	9
50	241.2	242.6	242.6	124.6	143.6	120.4			
49	212.8	146.4	106.6	102.6	119.4	106.4			
53	397.2	274.2							
36	88.2	85.6	145.6	121.4	171,6	126.6	156.4	204.2	194.2
66	376.2	396.6	362.6	287.8					

(f) Bu frequency

S	1	2	3	4	5	6	7	8	9
50	45	68	57	37	39	40			
49	67	53	48	36	50	36			
53	97	94							
36	46	37	31	35	62	78	50	51	54
66	138	141	133	141					

(g) Bu duration

S	1	2	3	4	5	6	7	8	9
50	0	11	12	3.6	6	1.6			
49	38.8	33.2	65.4	89.2	80.8	91			
53	15	36.8							
36	151.2	232.8	192.4	294.8	171.8	301.2	250.8	186.4	200
66	155.0	156.8	261.8	154.8					

Table 3 continued

(h) Bi frequency

S	1	2	3	4	5	6	7	8	9
50	1	10	6	6	13	10			
49	26	17	34	51	40	39			
53	18	21							
36	16	23	19	22	12	23	19	21	21
66	21	35	36	48					

(i) AG frequency

S	1	2	3	4	5	6	7	8	9
50	39	56	41	47	47	42			
49	49	54	67	55	65	69			
53	50	63							
36	25	33	35	35	13	17	26	14	21
66	45	22	21	31					

(j) AG duration

S	1	2	3	4	5	6	7	8	9
50	283.8	169	170.4	199.6	206.6	193.8			
49	22.2	209.4	300.2	200.2	207.8	243.6			
53	144	210.8							
36	47.0	46.8	139.8	74.0	17.8	25.6	23.6	16.8	33.2
66	52.8	38.2	21.8	42.6					

Table 4

Mean frequency of behaviours to a subordinate over days.

Significance testing by Friedman 2-way analysis of variance.

	Day	1	2	3	4	5	6	7	8	9	Chi	p
FD	$\bar{X}$	53	63	60.5	53.8	53.3	44.9	31.1	41.9	61.4		
	SEM	16.7	23.0	20.6	19.1	20.4	13.0	9.2	13.4	17.0	4.98	p>.70
LD	$\bar{X}$	58.9	64.5	61.8	55.3	55.6	46.6	37.9	46.4	65.4		
	SEM	16.1	20.6	20.8	20.9	21.2	14.2	11.9	13.6	18.6	6.60	p>.50
AG	$\bar{X}$	23.1	17.3	19.1	18.6	13.9	16.8	15.9	15	17.4		
	SEM	3.9	3.5	3.7	3.7	2,9	3.0	2.7	2.9	4.2	11.22	p>.10
Bu	$\bar{X}$	5.9	10.4	9.5	9.6	5.6	9.1	6.6	7.8	11.9		
	SEM	2.5	7.2	6.1	5.5	3.4	4.6	5.5	5.2	5.2	5.81	p>.50
Usw	$\bar{X}$	52.3	50	67	61.9	52	59.4	60.5	73.1	66.1		
	SEM	27.8	28.9	33.0	31.0	24.1	27.4	28.5	30.8	28.8	2.34	p>.95
StME	$\bar{X}$	51.9	60.3	61.8	59.4	52.1	55.1	58.4	60.3	55.1		
	SEM	25.2	26.5	28.2	27.0	24.2	25.6	21.1	28.3	27.2	4.67	p>.70
Wls	$\bar{X}$	29.1	29.9	28.7	21.5	20.9	17.1	21.6	19.1	20.6		
	SEM	12.8	10.7	10.2	6.6	7.6	6.1	8.5	8.1	7.0	8.12	p>.30
Bi	$\bar{X}$	2.9	1.5	1.8	1.1	0.9	1.5	0.4	1.1	2.3		
	SEM	2.1	.8	.9	.6	.4	.5	.8	.7	.9	4.47	p>.80
Wi	$\bar{X}$	20.7	19.3	23.1	20.6	20.0	20.1	18.8	19.8	24.3		
	SEM	6.6	6.7	7.8	6.8	6.8	6.6	7.7	5.4	8.9	3.02	p>.90

df = 8
N = 8

Table 5

Mean durations (secs.) of behaviours to a subordinate over days. Significance testing by Friedman 2-way analysis of variance.

	Day	1	2	3	4	5	6	7	8	9	Chi	p
FD	$\bar{X}$	134.7	127.6	112.8	103.1	94.6	89.5	71.6	92.7	127.5		
	SEM	54.8	55.2	50.3	47.1	41.6	39.0	27.7	36.4	49.7	6.57	p>.50
LD	$\bar{X}$	185.8	164.6	162.5	148.8	155.2	158.9	138.6	161.7	196.2		
	SEM	66.3	69.5	75.5	76.7	76.3	75.2	70.8	67.5	79.0	5.87	p>.50
AG	$\bar{X}$	38.6	22.8	30.1	22.0	22.9	23.7	20.5	21.8	23.8		
	SEM	13.1	8.2	11.8	7.7	9.8	12.4	7.8	8.4	11.9	15.78	p<.05
Bu	$\bar{X}$	11.0	18.6	21.5	18.5	15.0	19.3	16.2	18.3	23.7		
	SEM	5.9	13.2	14.6	11.1	12.4	13.2	12.7	12.9	12.1	2.95	p>.90
Usw	$\bar{X}$	72.0	67.7	94	68.3	67.4	63.6	65.5	66.6	69.1		
	SEM	31.0	30.3	44.1	30.3	27.9	26,6	27.9	26.9	30.4	3.18	p>.90
StME	$\bar{X}$	160.6	169.5	131.8	167.3	123.1	148.7	158.5	149.6	117.7		
	SEM	55.2	56.6	54.2	73.0	56.1	67.2	54.9	61.8	52.1	9.54	p>.20
Wls	$\bar{X}$	104.2	110.3	81.3	81.8	58.4	45.3	61.3	38.2	55.6		
	SEM	47.0	38.3	32.0	26.0	24.0	23.0	26.5	17.0	23.4	8.00	p>.30

		1	2	3	4	5	6
Total behaviour durations (secs.)	$\bar{X}$	693.9	681.1	634.7	581.7	536.6	548.8
	SEM	64.1	78.1	99.9	105.9	101.1	111.2

	7	8	9	Chi	p
$\bar{X}$	532.2	548.9	632.5		
SEM	97.8	99.2	341.6	12.77	p>.10

df = 8
N = 8

Table 6

Comparisons of mean frequencies of behaviours to the three subordinate stimuli (A, B and C).

Significance testing by Friedman 2-way analysis of variance.

Stimulus		A	B	C	Chi	p
FD freq	$\bar{X}$	77.4	56	67.1		
	SEM	24.3	20.9	21.7	0.06	p>.967
LD freq	$\bar{X}$	79.8	51.9	69.4		
	SEM	25.6	17.3	21.8	3.06	p>.236
AG freq	$\bar{X}$	24.1	19.8	20.9		
	SEM	5.3	6.2	4.0	1.19	p>.531
Bu freq	$\bar{X}$	5.6	16.4	4.0		
	SEM	2.9	8.5	1.6	0.44	p>.794
Bi freq	$\bar{X}$	2.0	1.6	3.3		
	SEM	.9	.9	1.5	0.81	p>.654
Wi freq	$\bar{X}$	11.5	12.3	21.1		
	SEM	5.6	5.4	5.3	3.06	p>.236
Wls freq	$\bar{X}$	28.5	13.8	28.1		
	SEM	11.9	7.7	9.5	3.06	p>.236
Usw freq	$\bar{X}$	54.6	40.4	65.1		
	SEM	23.6	19.8	17.8	4.00	p=.149
StMe freq	$\bar{X}$	49.4	36.1	60.9		
	SEM	19.7	16.9	17.1	4.00	p=.149
TB freq	$\bar{X}$	28.5	13.8	28.1		
	SEM	11.9	7.7	9.5	3.06	p>.236
NB freq	$\bar{X}$	1.9	6.3	6.4		
	SEM	1.3	3.1	3.2	3.06	p>.236
NP freq	$\bar{X}$	1.1	.9	2.4		
	SEM	.9	.8	2.5	0.06	p>.967
Fan freq	$\bar{X}$	2.1	3	.6		
	SEM	1.8	2.9	.4	0.25	p=.967

k = 3
N = 8

Table 7

Comparisons of mean durations of behaviours to the three subordinate stimuli (A, B and C).

Significance testing by Friedman 2-way analysis of variance.

Stimulus		A	B	C	Chi	p
FD secs	$\bar{X}$	125.1	142.4	106.3		
	SEM	46.9	73.1	47.4	0.81	p>.654
LD secs	$\bar{X}$	221.1	122.5	183.0		
	SEM	91.8	49.6	76.8	0.25	p=.967
AG secs	$\bar{X}$	56.2	41.0	32.8		
	SEM	37.1	24.8	14.3	0.75	p=.794
Bu secs	$\bar{X}$	7.4	32.9	5.0		
	SEM	4.4	18.2	2.5	0.25	p=.967
Wls secs	$\bar{X}$	118.4	53.7	88.9		
	SEM	54.1	31.4	29.8	0.44	p>.794
Usw secs	$\bar{X}$	64.6	44.8	84.2		
	SEM	26.5	19.8	25.9	3.25	p=.236
StME secs	$\bar{X}$	160.7	98.2	208.6		
	SEM	67.1	42.9	71.6	5.25	p=.531
NB secs	$\bar{X}$	16.7	133.2	61.5		
	SEM	12.8	82.2	42.0	1.56	p>.531
NP secs	$\bar{X}$	6.5	7.4	19.8		
	SEM	6.4	7.7	21.1	0.06	p>.967
Fan secs	$\bar{X}$	14.1	56.2	4.3		
	SEM	11,5	58,5	2.6	0.25	p=.967

k = 3
N = 8

Table 8

Comparisons of the frequencies of behaviours to subordinate stimuli in the three serial positions (1, 2 and 3).

Significance testing by Friedman 2-way analysis of variance.

Serial position :	1	2	3	Chi	p
FD freq $\bar{x}$:	72.4	57.3	70.9		
FD freq SEM :	23.1	18.8	25.1	0.44	p>.794
LD freq $\bar{x}$:	71.0	51.5	72.5		
LD freq SEM :	22.6	17.1	25.6	0.19	p>.967
AG freq $\bar{x}$:	25.3	20.4	19.1		
AG freq SEM :	5.4	5.5	4.7	1.56	p>.531
Bu freq $\bar{x}$:	7.5	9.5	9.0		
Bu freq SEM :	6.0	5.0	6.1	0.06	p>.967
Bi freq $\bar{x}$:	1.1	2.3	3.5		
Bi freq SEM :	0.7	0.9	1.4	1.31	p>.531
TB freq $\bar{x}$:	28.3	23.0	19.1		
TB freq SEM :	11.1	10.4	8.7	0.44	p>.794
Wi freq $\bar{x}$:	13.3	15.1	16.5		
Wi freq SEM :	5.0	6.1	5.8	0.00	p=1.00
Wls freq $\bar{x}$:	28.3	23	19.1		
Wls freq SEM :	11.1	10.4	8.7	0.44	p>.794
Usw freq $\bar{x}$:	42.6	67.1	50.4		
Usw freq SEM :	14.8	26.5	18.6	0.81	p>.654
StME freq $\bar{x}$:	42.3	57.6	46.5		
StME freq SEM :	14.6	22.8	16.0	0.19	p>.967
NB freq $\bar{x}$:	1.5	7.1	5		
NB freq SEM :	1.2	3.5	2.8	2.44	p>.285
NP freq $\bar{x}$:	0.9	1.1	2.1		
NP freq SEM :	0.9	0.8	2.4	0.25	p=.967
Pan freq $\bar{x}$:	1.9	3.3	0.5		
Pan freq SEM :	1.9	2.9	0.4	1.75	p=.531

k = 3
N = 8

Table 9

Comparisons of the durations of behaviours to subordinate stimuli in the three serial positions (1, 2 and 3).

Significance testing by Friedman 2-way analysis of variance.

Serial position		1	2	3	Chi	p
FD secs	$\bar{X}$	154.0	122.9	96.7		
	SEM	62.6	63.0	41.6	0.44	p>.794
LD secs	$\bar{X}$	202.6	118.0	206,0		
	SEM	73.8	53.7	92.0	1.75	p=.531
AG secs	$\bar{X}$	36.2	53.5	40.3		
	SEM	13.9	37.7	24.4	1.19	p>.531
Bu secs	$\bar{X}$	11.0	23.7	10.6		
	SEM	9.8	15.8	8.5	0.19	p>.967
Wls secs	$\bar{X}$	136.2	63.3	61.5		
	SEM	53.3	27.7	30.6	2.31	p>.285
Usw secs	$\bar{X}$	56.8	75.5	61.2		
	SEM	20.2	29.1	24.6	0.44	p>.794
StME secs	$\bar{X}$	126.7	162.8	139.3		
	SEM	49.1	67.4	66.8	0.06	p>.967
NB secs	$\bar{X}$	14.4	70.0	127.2		
	SEM	12.3	36.7	85.2	4.19	p>.149
NP secs	$\bar{X}$	6.1	8.0	19.8		
	SEM	6.5	7.5	21.1	1.00	p=.654
Fan secs	$\bar{X}$	10.8	59.6	4.3		
	SEM	11.5	58.0	2.6	2.44	p>.285

k = 3
N = 8

Table 10

Comparisons of frequencies (freq.) and durations (secs.) of behaviours in nest intact (N) and nest removed(NR) groups responding to a male subordinate. Significance testing was by Mann-Whitney U test. N = 8 for each group. * denotes a significant effect 2-tailed, in opposite direction to that predicted.

	FD freq.		FD secs.		LD freq.		LD secs.	
	N	NR	N	NR	N	NR	N	NR
$\bar{x}$	50.4	34.6	98.5	41.2	55.6	43	77.6	42.1
SEM	8.3	9.3	23.9	14.7	8.2	7.7	20.9	10.1
u,u'	15,49		12,52		19,45		17,47	
p (1-tailed)	=.041		=.109		N.S.		N.S.	
p (2-tailed)	N.S.		=.038*					

	Bu freq.		Bu secs.		TBfreq.		Bi freq.	
	N	NR	N	NR	N	NR	N	NR
$\bar{x}$	4.9	2.5	9.1	2.8	0.8	0.6	0.4	1.3
SEM	2.6	1.8	5.9	2.5	0.4	0.5	0.3	1.2
u,u'	19,45		17,47		28.5,35.5		31.5,32.5	
p (1-tailed)	N.S.		N.S.		N.S.		N.S.	

	AG freq.		AG secs.		Wls secs.		Wls secs.	
	N	NR	N	NR	N	NR	N	NR
$\bar{x}$	15.3	12.8	6.1	6.5	45.5	41.3	210.4	147.3
SEM	1.4	1.1	1.1	0.7	8.4	8.0	42.7	17.0
u,u'	16.5,47.5		22,42		22.5,41.5		21,43	
p (1-tailed)	N.S.		N.S.		N.S.		N.S.	

	STME freq.		STME secs.		Usw freq.		Usw secs.	
	N	NR	N	NR	N	NR	N	NR
$\bar{x}$	99	124	186.9	259.0	101.6	134.8	83.7	133.0
SEM	29.0	27.6	54.9	40.3	28	31.7	19.8	28.2
u,u'	23,41		21,43		22,42		20,44	
p (1-tailed)	N.S.		N.S.		N.S.		N.S.	

	Wi freq.	
	N	NR
$\bar{x}$	34.5	39.5
SEM	5.4	4.6
u,u'	27,37	
p (1-tailed)	N.S.	

Table 11

Comparisons of frequencies (freq.) and durations (secs.) of behaviours in nest building males presented with male subordinates (N) and reproductive females (NF).

Significance testing by Mann-Whitney U test. N = 8.

	FD freq		FD secs		LD freq		LD secs	
	N	NF	N	NF	N	NF	N	NF
$\bar{X}$	50.4	32.8	98.5	65.8	55.6	38.5	77.6	153.6
SEM	8.3	7.4	23.9	18.7	8.2	6.8	20.9	80.4
U,U'	15,49		21,43		15.5,48.5		29,35	
p(2-tailed)	N.S.		N.S.		N.S.		N.S.	

	Bu freq		Bu secs		TB freq		Bi freq	
	N	NF	N	NF	N	NF	N	NF
$\bar{X}$	4.9	2.8	9.1	5.1	0.8	0.1	0.4	1.3
SEM	2.6	2.2	5.9	4.9	0.4	0.1	0.3	0.8
U,U'	20,44		20,44		23.41		26.5,37.5	
p(2-tailed)	N.S.		N.S.		N.S.		N.S.	

	AG freq		AG secs		Wls freq		Wls secs	
	N	NF	N	NF	N	NF	N	NF
$\bar{X}$	15.3	11.1	6.1	7.0	45.5	30.3	210.4	228.3
SEM	1.4	2.6	1.1	1.1	8.4	5.6	42.7	55.1
U,U'	15,49		23,41		16.5,47.5		32,32	
p(2-tailed)	N.S.		N.S.		N.S.		N.S.	

	StME freq		StME secs		Usw freq		Usw secs	
	N	NF	N	NF	N	NF	N	NF
$\bar{X}$	99	68.4	186.9	127	101.6	81.9	83.7	84.1
SEM	29.0	28.8	54.9	41.6	28.0	27.7	19.8	21.6
U,U'	25,39		26,38		32,32		26.5,37.5	

	Wi freq	
	N	NF
$\bar{X}$	34.5	
SEM	5.4	
U,U'	26.5,37.5	
p(2-tailed)	N.S.	

CHAPTER 6

6.1 Operant Conditioning - General Methods

Since the experiment reported in ch. 5.10 demonstrated that the initial behaviour which occurs between displaying males can be sexual in causation, it is likely that such behaviour will also occur between the subjects in an operant experiment and the displaying conspecifics used as reward stimuli. Since intermale courtship involves the operation of a motivational system whose mode of functioning may be quite different from that of aggressive display, difficulties of interpretation could arise if such behaviour is allowed to occur in an operant situation. A study of aggression reinforcement should attempt to minimise the roles of other motivational systems including that controlling sexual behaviour.

Not only subjects but stimulus males also may be initially sexually motivated when presented with a conspecific. When this occurs in stimulus fish it takes a distinctive form. The fish in its container adopts display coloration (i.e. it is not submissive) but it rarely erects its gill covers and does not show regular alternations between frontal and lateral display. Instead it spends much time facing away from the subject and makes swimming movements as if to withdraw from the subject through the container wall. This may be an extremely vigorous behaviour. Because it shows little gill cover erection, the stimulus may not have a stimulating effect on the attack tendency of the subject. Although the use of a live stimulus male allows a great deal of variability in the reward stimulus, this variability is small compared to that which would exist if stimulus fish were used which varied greatly in their sexual tendencies. For this reason, a stimulus fish priming procedure will be used in the following experiments to ensure that stimulus fish behave agonistically when presented to subjects.

To produce a transition from initially sexual to agonistic behaviour, both subjects and stimulus fish were preexposed

to a displaying male conspecific. This procedure, which differs for subjects and stimulus fish will be referred to as subject or stimulus pretreatment. Stimulus pretreatment will be described first.

6.1 (a) Stimulus Pretreatment

In addition to the stimulus selection test (see ch. 5.2(b)) being used to select displaying reinforcer males it is also used to select two males who will display without withdrawals to all stimulus males. These stimulus pretreatment males are moved to experimental maintenance conditions in the same way as subject and stimulus males. Before each experimental session stimulus fish were treated as follows: A stimulus pretreatment male was inserted into the home tank of the stimulus fish. Neither fish was restrained during this procedure. If the stimulus male showed no disposition to respond to the male with withdrawals then after the first 3 frontal displays by the stimulus fish it was removed and placed in the stimulus container. The preliminary experimental procedure (pre-feeding etc.) then continued as for previous experiments. If the stimulus fish did withdraw from the pretreatment fish then it would normally be followed around the tank by the frontally displaying pretreatment male. Eventually the stimulus fish would remain within one fish length of the pretreatmant fish and perform three frontal displays without an intervening withdrawal. After this procedure it is unlikely that stimulus fish will show sexual behaviour during the following operant session. At this point the stimulus fish was netted and placed in the stimulus container. The priming male was then returned to its home tank. The preliminary experimental procedure then continued as for the previous experiments. The two stimulus pretreatment males were used in alternation to prevent dominance over them being established. No biting ever occurred during this stimulus pretreatment procedure and no such procedure lasted more than three minutes.

Having been pretreated, the stimulus male was carried in the stimulus container to the test chamber where it was placed under the stimulus cover and lowered into the subject's tank as before.

6.1 (b) Subject Pretreatment

At this point the subject pretreatment was carried out so that no courtship would be shown during reinforcements. This was achieved as follows:

In general room illumination the stimulus cover was raised manually exposing the stimulus fish and the behaviour of the subject was observed. Simultaneously, two Smiths mechanical timers were started. One timer was reset each time the subject showed withdrawal (Wi) from the stimulus fish. When no withdrawal had been made for a period of 30 seconds both timers were stopped and the cover lowered. The time to this criterion as read from the first timer was noted and one minute later the operant session proper began.

6.2 Apparatus

6.2 (a) Reward Presentation

The apparatus used in the preceding experiments allowed the conspecific stimulus to be presented automatically by the raising of the stimulus cover. Stimulus presentation and termination were controlled directly by the experimenter throwing a switch and activating the motor which raised the stimulus cover. In the present experiment, instead of presentation durations being 15mins. and controlled by the experimenter, a system of electromechanical and solid state logic housed remote from the experimental room raises the cover and holds it up for 30secs., after which time it is lowered again. This stimulus presentation is contingent on a reed switch being closed and then reopened. The opportunity to close this switch must be available to the experimental subject if the apparatus is to be used for

operant experiments. A suitable operandum was therefore required.

6.2 (b) The Operandum

A rectangular block of black plexiglass 12 x 8 x 1.5cms., with a central rectangular aperture 3 x 3.5cms., acted as a response gate, the subject swimming through the aperture. In both short sides of this block were drilled two holes into which were sealed a pair of 1.5w. bulbs on one side and a pair of photoelectric cells on the other side. Waterproofing was by means of an epoxy resin. This apparatus is schematically represented in Fig. 18.
The arrangement of the photocells was such that a male Betta splendens could not swim through the aperture in the plexiglass block (performing an operant response) without breaking one or both of the light beams which traversed it.

From the top side of the block ran a brass rod 28cms. long and 3mm. in diameter, from which the block could be suspended. The end of this rod was fitted into a hole drilled in the hinged transparent lid of the test chamber and fixed into a flat bar of plexiglass lying on its side and bolted to the lid upper surface. The leads running from the photocells and bulbs ran through plastic piping and were attached to the brass rod, these passed through the test chamber roof via the same hole as the rod. (see Fig. 18). Both rod and the accompanying wiring were bound in black adhesive tape. The plexiglass bar when fixed onto the end of the rod and bolted to the hinged roof of the test chamber allowed the raising of the lid to lift the operandum clear of the subject's tank. Fig. 18 shows the position of the operandum within the subject's tank relative to the stimulus cover, and its position when the test chamber lid was raised. When in the tank the distance from the centre of the response gate aperture to the nearest point of the stimulus cover was approximately 18cms.

6.2 (c) Controlling Circuitry

The electromechanical and electronic circuitry was arranged so that a 30sec. stimulus presentation (a reinforcement) was delivered whenever either or both light beams in the operandum were broken and then remade. This occurs when the subject fish swims through a response gate and then swims out again. The beam must be broken for .5secs. before the response is registered and a reward delivered. The breaking of the beam during a reinforcement presentation had no consecuences.

6.2 (d) Data Recording

The time of occurrence of responses and reinforcements were recorded on a Sodeco printing counter. In addition a cumulative record of responses and reinforcements was produced by a Campden Instruments pen recorder. Both of these recording devices were programmed to ignore the time during which reinforcements were being delivered. The length of a test session and the time of occurrence of responses and rewards were exclusive of the time consumed by reward. This practice is not usual in operant experiments but allows a more accurate measure of a subject's response rate, since it is based only on the time during which the fish is free to respond. Initiation of an operant session was accomplished by the experimenter throwing two switches on the table in front of the test cubicle. The first switch activated the photocells in the response gate and the second activated the controlling logic circuitry and lighted the test chamber lamp.

The first response of the subject activated an electronic timer connected to a digital counter on the table in front of the experimenter, which indicated time in secs. since the first response. A pair of similar counters incremented with each response and reinforcement during a test session. A duplicate set of counters similarly activated were located with the controllong circuitry remote from the experimental room. Operant sessions could be terminated and the chamber

light extinguished by switches in the experimental room or at the remote controlling logic.

Figure 18

The operant situation.

a Test chamber.

b Subject's tank.

c Stimulus cover.

d Response gate (operandum).

e Test chamber lid (closed).

f Test chamber lid (open).

f
d
c
e
b
a

CHAPTER 7

7.1 The Motivating Effects of Conspecific Presentation

A session of aggression reinforcement involves a series of presentations of an aggression eliciting stimulus, presentations being contingent of the performance of an operant response. The aim of the following studies is to discover the relations between the aggressive behaviour occurring during reinforcement and the rate and patterning of operant behaviour for such reinforcements.

One way of approaching this problem is to attempt to relate the changes in display and attack behaviour which occur during normal fights with changes in operant response rate occurring during a session of aggression reinforcement. If, for example, the rate of attacks directed at a male conspecific during an aggressive encounter progressively increases, then an increase in attack would also be expected to occur over successive rewards in an operant situation. If attack is involved in the motivation of responding for aggression reward, then an increase in operant response rate would be expected to accompany this increase in attack.

Considering first the possibility of changes in attack behaviours occurring during a continuous aggressive encounter, evidence exists to suggest that in many species such a change does occur and involves a progressive increase in the levels of attack into the fight (e.g.
for sticklebacks: Sevenster, 1961; for the Cyprinodont Aphyosemion striatum: Dow, Ewing and Sutherland, 1976). Heiligenberg (1965) has investigated this facilitation of attack in detail for the cichlid Pelmatochromis kribensis. In this species the presentation of a dummy resembling a conspecific male raises the attack rate of subject males to a level above that expected without dummy presentation, and this elevation of attack readiness persists for some time after the dummy is withdrawn. Such stimulation was shown to cause an excitory process which reaches its peak within the first minute after stimulation and thereafter decays with a half-time of approximately 1.5mins. This increment in attack

rate can be described as being additively superimposed on the level of attack readiness expected without stimulation. In the cichlid Haplochromis burtoni, Heiligenberg, Kramer and Shulz (1972) found the size of the increment in attack rate produced by dummy presentation depends on a particular stimulus characteristic of the dummy, namely the angular orientation of the black eye-bar with respect to the forehead. The more parallel this eye-bar and the forehead profile, the higher the increment in attack rate the dummy will produce.

That some attack facilitation processes, perhaps similar to those outlined above for cichlids, are operating in Betta splendens fighting is suggested by the repeated observation that Bettas, male and female, do not attack at a uniform rate throughout fights. Instead attack does not occur until several minutes into the fight. Laudien (1965) suggests that the various components of the fighting behaviour of Betta splendens depend on different levels of a single "aggressiveness" variable for their occurrence. If jawlocking is not considered, biting occurs at the highest level of aggressiveness being the behaviour with the greatest latency. Hogan (1961) considers that this increase in aggressiveness due to conspecific presentation is not stimulus specific, since fish also respond more strongly (in terms of display or attack) to a thermometer or finger inserted into their tank. Several workers have measured the latency to attack during fights between Bettas, both male and female. Simpson (1968) (for males) and Braddock & Braddock (1955) (for females) found a median latency to the first rapid exchange of bites between combatants to be between four and eight minutes. That after this initial latency, attack progressively increases has been shown by Laudien (1965) who reports that biting in two male Bettas reached its peak at the ninth minute of a fight. If only single bites are considered rather than mutually exchanged bites, Simpson(s (1968) data reveals that the mean latency to the first bite (of the 14 subjects which showed biting) is 3.6mins. Facilitation in some display components has also

been reported by Clayton and Hinde (1968) and Chantry (1978).

It seems to be well established that attack in Betta splendens is not randomly distributed throughout the fight but may have a latency of several minutes before its first occurrence and may increase thereafter. The work of Heiligenberg and his associates described above also suggests the possibility that the facilitatory processes underlying the increase in attack observed in Betta splendens may involve excitation which decays on removal of the eliciting stimulus. The implications of any such process for behaviour in an operant situation which involves discrete stimulus presentations will be fully considered later (ch.10).

The identification by Heiligenberg et al.(1972) of a particular stimulus characteristic in Haplochromis burtoni which determines the effect of a conspecific on the aggressive tendencies of other fish, raises the questions about particular stimulus characteristics of Betta splendens which might facilitate attack in an opponent. The results of Experiment ? in the present thesis, in which fish who showed a high level of display to subordinates showed a simultaneously low level of biting, suggests that display on the part of the opponent or perhaps the absence of subordinate stripes are necessary for attack to be elicited. It was also suggested that display and attack might be under the control of different mechanisms. The possibility of differences between the various displays of the actor having different effects on the attack readiness of the receiver has not been investigated and neither has the precise nature of the excitory and decay processes which may control attack behaviours.

In the experiments to be discussed in this chapter a working hypothesis was adopted which states that attack tendencies are involved in the motivation of operant responses for display reward. This hypothesis was tested first indirectly by looking for evidence of changes in attack probability during continuous rival presentations outside

the operant situation, and then looking for a similar pattern of change in operant responding in a separate operant experiment. More direct evidence for a link between attack tendencies and operant responding was sought in a later analysis in which changes in attack behaviour over successive aggression rewards were related to changes in operant responding for those same rewards.

7.2 The Course of Attack Within An Aggressive Encounter: Further Analysis of Experiment 1

7.2 (a) Introduction

Does the probability of attack increase during an aggressive encounter between male Bettas? The previous discussion suggests that it does. The following section will seek to confirm this by re-analysing the data generated by Experiment 1 in which displaying males were presented to subjects and their behaviour observed for 15 consecutive minutes. Since several measures of attack can be used (biting frequency, butting frequency and duration), the degree to which these are related can also be investigated. It was hypothesised that all measures of attack would be positively correlated.

7.2 (b) Method

In Experiment 1, subjects were presented with displaying and subordinate males for nine consecutive days (ch. 5.2). For each of the seven subjects, data for the first day of presentation of displaying males was re-analysed to reveal any changes in the rate of attack behaviours (biting and butting) as the 15min. session proceeded. For each successive 1min. interval of the session the number of bites and butts and the duration of butts were calculated. The statistical significance of changes in these behaviours was determined by correlating the mean amounts of each behaviour occurring

during successive one minute intervals. In addition, the means of the two measures of butting (frequency and duration) were correlated with each other and with biting frequency over successive one minute intervals. The correlation method used was Spearman's Rank Order correlation. Significance testing was 1 - tailed since the hypothesis involves the prediction of a positive correlation between the various attack behaviours and between these behaviours and the serial order of the observation interval.

7.2 (c) Results

Fig. 19 shows the course of biting over successive 1min. intervals of testing. The mean number of bites emitted by subjects per minute was 0 until the 3rd minute of observation and thereafter rose rapidly until the 6th minute at which it reached an asymptote. The correlation between mean number of bites during 1min. intervals and the serial order of those intervals was .6014 (Spearman. $p < .05$, 1 - tailed).

Fig. 20 shows that butting frequency and duration also increased into the session, and were significantly positively correlated with the interval serial order. r_s = .7314 and .8674, respectively. From the 4th to the 6th minute, butting frequency increased rapidly and thereafter more slowly. Butting duration continued to increase until the 12th minute. Both butting and biting had mean latencies of between 5 and 6 minutes. The correlation between biting and the two measures of butting were all positive and significant (table 12).

7.2 (d) Discussion

Biting and butting did not occur until several minutes into encounters and the mean rates of biting and butting, and the mean duration of butting increased as the observation period proceeded. These results support the hypothesis

that continued exposure of a male Betta to a displaying male conspecific increases its rate of attack. The high correlations between attack behaviours also suggest that it may not be necessary to postulate more than a single attack tendency to account for all measures of attack.

7.3 The Course of Operant Responding Within Sessions

7.3 (a) Introduction • Experiment 5

The previous analysis showed that outside the operant situation encounters between pairs of male Bettas are characterized by a ~~progressive~~ increase in the rate of attack behaviours. It was earlier suggested that if operant behaviour for display reward were motivated by attack tendencies and if attack increased during operant sessions for display reward, then a concomitant increase in operant response rate should be found. The course of operant responding during experimental sessions has been elsewhere investigated only in a limited way. Using a target pressing response, Hogan and Rozin (reported in Hogan and Roper, 1978, p. 193) found that operant response rate for mirror image reward did increase as the operant session progressed. To support this statement, data is presented for a single Betta for one session, showing that an initial acceleration in response rate occurred and that this was followed by a decline in responding towards the end of the session. No statistical treatment of the data is reported.

The following experiment will test the hypothesis that operant response rate increases during test sessions. Subsequent experiments will seek to confirm that attack increases not only during long (15min) encounters as shown before, but also during operant sessions involving a series of short (30secs.) presentations as rewards.

Before any investigation of the control of operant responding can be carried out it is necessary to condition

Betta splendens to perform an operant response for display reward.

7.3 (b) Subjects and Stimulus Fish

Eleven male Betta splendens were randomly selected from those kept under initial maintenance conditions and having nest volumes of less than .4cms.^{3}. Some of these males had been used in previous experiments. Eleven displaying stimulus males were assigned to each of the 11 subjects such that each subject had a stimulus which displayed aggressively to it. This was achieved by means of the method used in Experiment 1 (ch. 5.2(b)) except that tests were 5mins long. Subjects which did not approach the stimulus within 5mins. who were subordinate to any stimulus male with which they were tested or who showed any withdrawals during the 4th and 5th minutes of the stimulus selection tests were rejected. This occurred in four cases and these were discarded and replaced. Subjects and stimulus males were then transferred to experimental maintenance conditions.

7.3 (c) Experimental Design

Subjects were given a session of operant level (O.L.) determination on two consecutive days at approximately the same time for individual subjects. O.L. is usually defined as the frequency with which the response occurs prior to reinforcement (after Skinner, 1938) but here a subject's operant level was the mean number of responses it emitted over 2 days of O.L. determination. O.L. sessions involved the same procedure as conditioning sessions, including subject and stimulus pretreatment, except that responses were not followed by reward. O.L. sessions were started 60secs. after the termination of subject pretreatment and were of 30mins. duration.

After 2 days of O.L. determination testing continued at the same time each day with each response being followed by reward. These acquisition sessions continued daily until

the subject had reached what appeared to be a stable daily rate of responding over 4 consecutive sessions. These sessions provided the data on which analysis was based. This stability in daily operant response rate was not determined by any criterion, but instead will be confirmed statistically later.

Any subject who did not exceed a response rate of 15 responses per 30min. session after 12 days of conditioning was discarded and replaced. This occurred for 4 subjects.

In the event of a subject's designated stimulus fish becoming subordinate before or during a session, that session was abandoned. Conditioning then continued on the following day with replacement of the stimulus fish. In such a case, data from sessions which had occurred before the change of stimulus fish were not included in the subject's 4 stable sessions, but instead data were collected for a further 4 consecutive sessions.

7.3 (d) Procedure

The preliminary procedure was as described in section 4.1 (d) with the stimulus fish pretreatment procedure described in 6.1 (a). The subject was carried in its home tank to the experimental room. The test chamber lid with its attached operandum was then raised and the subject's tank inserted. The stimulus male in its container was carried to the experimental chamber, and placed in the subject's tank under the stimulus cover. Subject pretreatment then took place, i.e. the stimulus cover was raised manually and the stimulus male exposed to the subject until the latter showed no withdrawals for 30secs. (see ch. 6.1(b)). The stimulus cover was then replaced and one minute later the test chamber lid was lowered, inserting the response gate into the subject's home tank. Immediately, by means of the two switches in front of the experimenter, the response gate photocells were activated, the chamber light illuminated and the remote response-recording and reinforcement apparatus switched on.

Operant session duration was 30mins. excluding the total reinforcement duration. Timing of conditioning sessions began with the subject's first operant response.

After 30mins. of testing, the chamber light was extinguished, the response-recording and reinforcement delivery apparatus was switched off, and the operandum removed from the subject's tank by raising the chamber lid. Subject and stimulus fish were then returned to experimental maintenance conditions as before.

For operant level determination, the procedure was identical except that reinforcement did not occur following operant responses, and sessions began 60secs. after subject pretreatment.

7.3 (e) Acquisition of the Operant Response - Results

The mean number of operant responses produced during operant level determination was 2.30 (SEM = .38), and the mean number of operant sessions required before subjects produced four consecutive sessions of stable responding was 3.9 sessions.

To determine whether the four consecutive sessions termed "stable" were indeed so, the differences between the numbers of responses performed by subjects during each of the four sessions were tested for significance by applying a Friedman analysis of variance. Table 13 reveals no significant differences between four sessions (Friedman, $p > .05$). The mean of the mean number of responses produced over the four stable sessions is 55.18 responses per session (including the first response of each session). It must be remembered that the test session duration of 30mins. is in this and subsequent operant experiments exclusive of reinforcement time.

7.3 (f) The Distribution of Inter Response Intervals - Results

For the response data generated by subjects during the

four days of stable responding, a frequency distribution of inter response intervals was generated. This was achieved by obtaining, for each subject the mean number of inter-response intervals (IRI's) excluding reinforcement time occurring within class intervals of 10secs., from 0 secs. to 120secs. and over. This was done for each of the four sessions for that subject. The mean frequency for each class interval was then calculated over the four sessions. Each subject had therefore a mean frequency distribution of inter-response intervals. Over subjects the grand mean for each class interval of this mean frequency distribution was calculated.

Fig. 21 shows the frequency polygon of the distribution of mean inter-response intervals. A result of interest is that very few IRI's of less than 10secs. occurred. Since 10secs. is an ample period of time for subjects to leave the reinforcement site and perform the nest operant response (a distance of 18cms.) the question of why most intervals are longer than this is of importance. In a later chapter (ch. 9) the possibility will be considered that performance of the operant response is inhibited by behaviour which immediately follows the reward.

7.4 Changes in the Rate of Operant Responding Within Sessions

7.4 (a) Method of Analysis

To test the hypothesis that the number of responses emitted by subjects increases into an operant session, each session was broken down into six successive five minute intervals and the number of responses occurring during each interval was calculated. The first response of each session (which initiated that session) was excluded from the number occurring during the first 5min. interval. This was performed for each subject for each of its four stable sessions and the mean number of responses for each subject which occurred during successive 5min. periods was computed.

In order to establish that any facilitation in operant response rate found in this analysis is not attributable to a progressive increase in responding over sessions it is necessary to show not only that the response rate at the end of a session was greater than at the beginning of that session but also that it was greater than the rate occurring at the beginning of the subsequent session (24 hours later). If the four stable sessions from which data were collected for each subject are termed sessions 1, 2, 3 and 4, then the mean number of responses of each subject for the first 10mins. of session 2, 3 and 4 can be compared with that subject's mean number of responses in the last 10 mins. of session 1, 2, and 3. The hypothesis is that more responses occurred in the last 10min. segments of the following sessions.

7.4 (b) Results

Fig. 22 shows that the mean number of responses (over 11 subjects) increased from the first 5min. interval to the 4th interval at which it reached an asymptote. Over all intervals the differences between intervals are significant (Fried., $p<.01$) and the difference between the first and last 5min. periods is significant (Wilcoxon, $p<.005$).

Fig. 22 also shows the numbers of responses occurring in successive 5min. segments of the last halves of operant sessions 1, 2 and 3 and the first halves of sessions 2, 3 and 4. Significant nonstationarity occurred over all segments (Fried., $p<.01$) the first halves of sessions (Fried., $p<.05$) but not over the last halves.

7.4 (c) Discussion

Operant response rate for aggression reward increased into sessions as predicted from knowledge of the changes in attack probability which occurred during aggressive encounters which did not involve an operant requirement. However, to

support further the hypothesis that operant responding for display reward and attack tendencies are linked, evidence is required that the increases in attack found in the above analysis also occur in the operant situation. If an increase in attack over successive rewards is accompanied by an increase in operant response rate for those rewards, then this will provide more direct evidence of a motivational link between the attack tendency and the learned behaviour. The following chapter considers the results of previous studies of the relations between the parameters of reward and operant responding and then reports the results of observation of reward elicited behaviours and analysis of the relations between these and operant behaviour.

Figure 19

The course of mean bite frequency (Bi) over successive minutes of rival presentation. Bars indicate one standard error.

Spearman correlation with minute of observation (1 - 15):

rho = .6014
N = 15
p(1-tailed) < .05

Figure 20

The course of mean butting frequency (Bu(f)) and duration (Bu(d)) over successive minutes of rival presentation. Bars indicate one standard error.

Spearman correlation with minute of observation (1 - 15):

	Bu (f)	Bu(d)
rho =	.7314	.8674
N =	15	15
p (1-tailed)	<.01	<.01

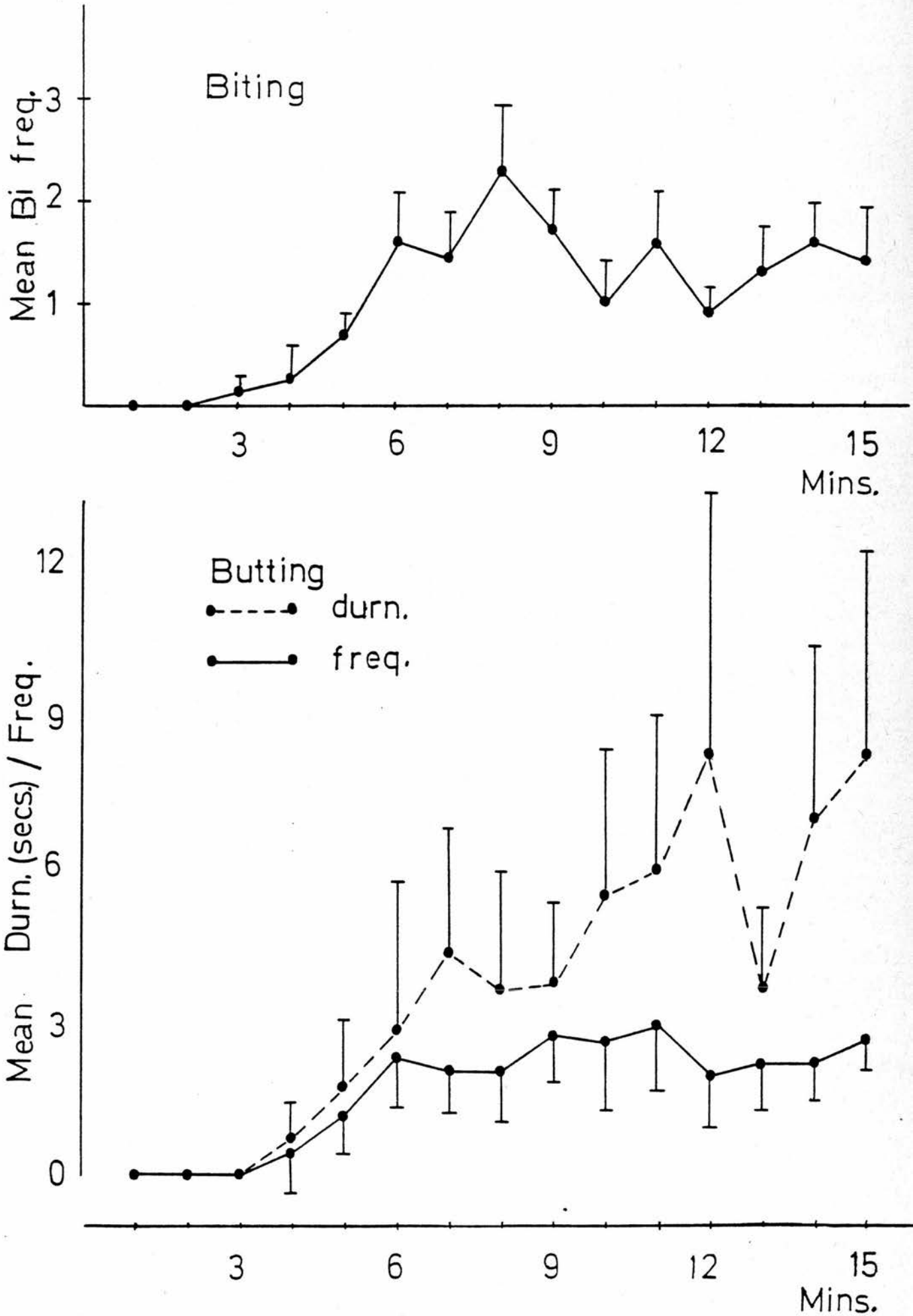

Biting
Mean Bi freq.
3
2
1
3
6
9
12
15
Mins.
Butting
durn.
freq.
Mean Durn. (secs.) / Freq.
12
9
6
3
0
3
6
9
12
15
Mins.

Figure 21

The mean frequency distribution of inter-response intervals (IRI's). N = 11.

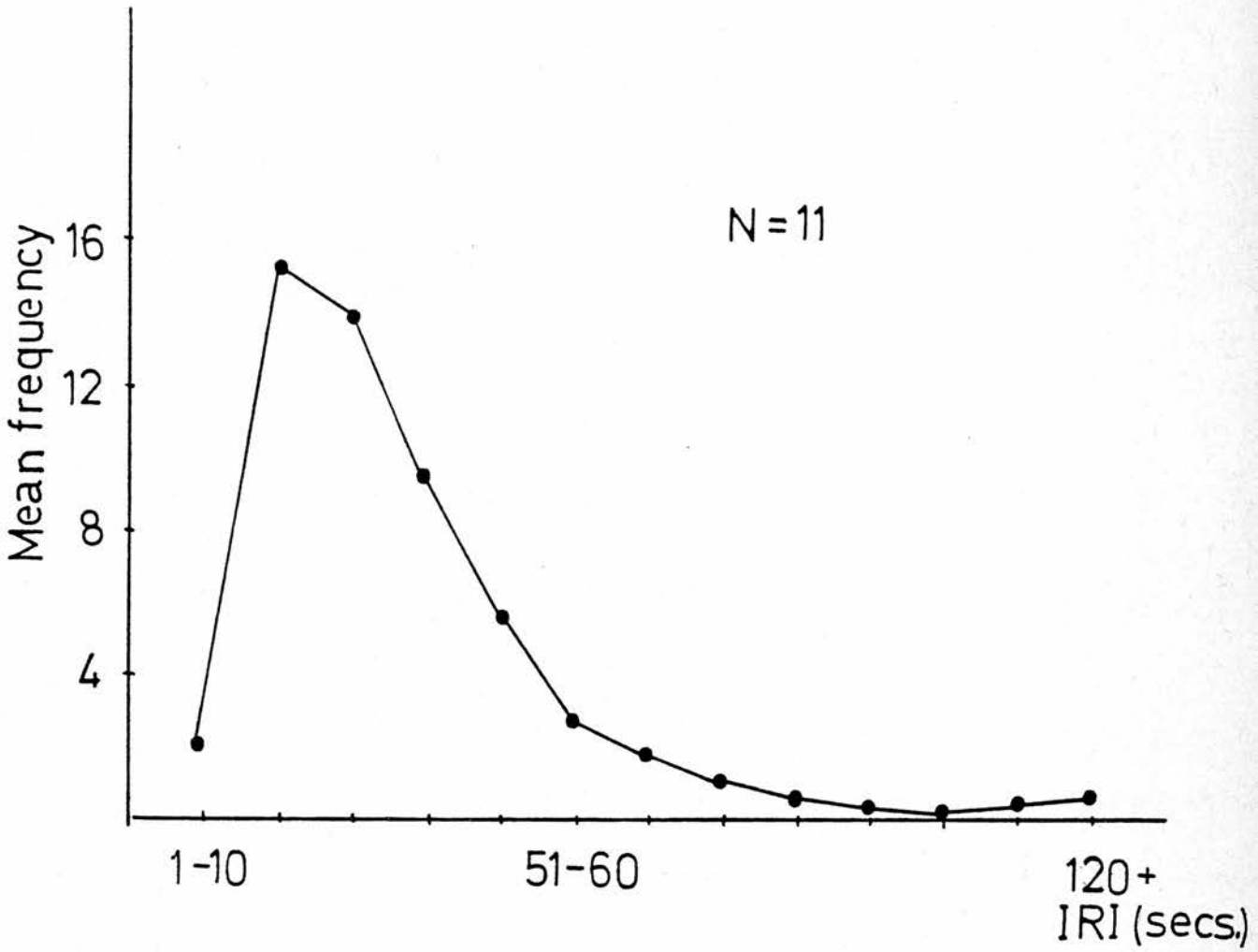

N = 11
Mean frequency
16
12
8
4
1-10
51-60
120+
IRI (secs.)

Figure 22

Mean number of operant responses in successive 5 min. segments of sessions. Significance testing by Friedman 2-way analysis of variance (N = 11). Bars represent two standard errors.

Chi = 20.1428

df = 5

$p < .01$

Comparison of first and last 5 min. segments by Wilcoxon test (1-tailed).

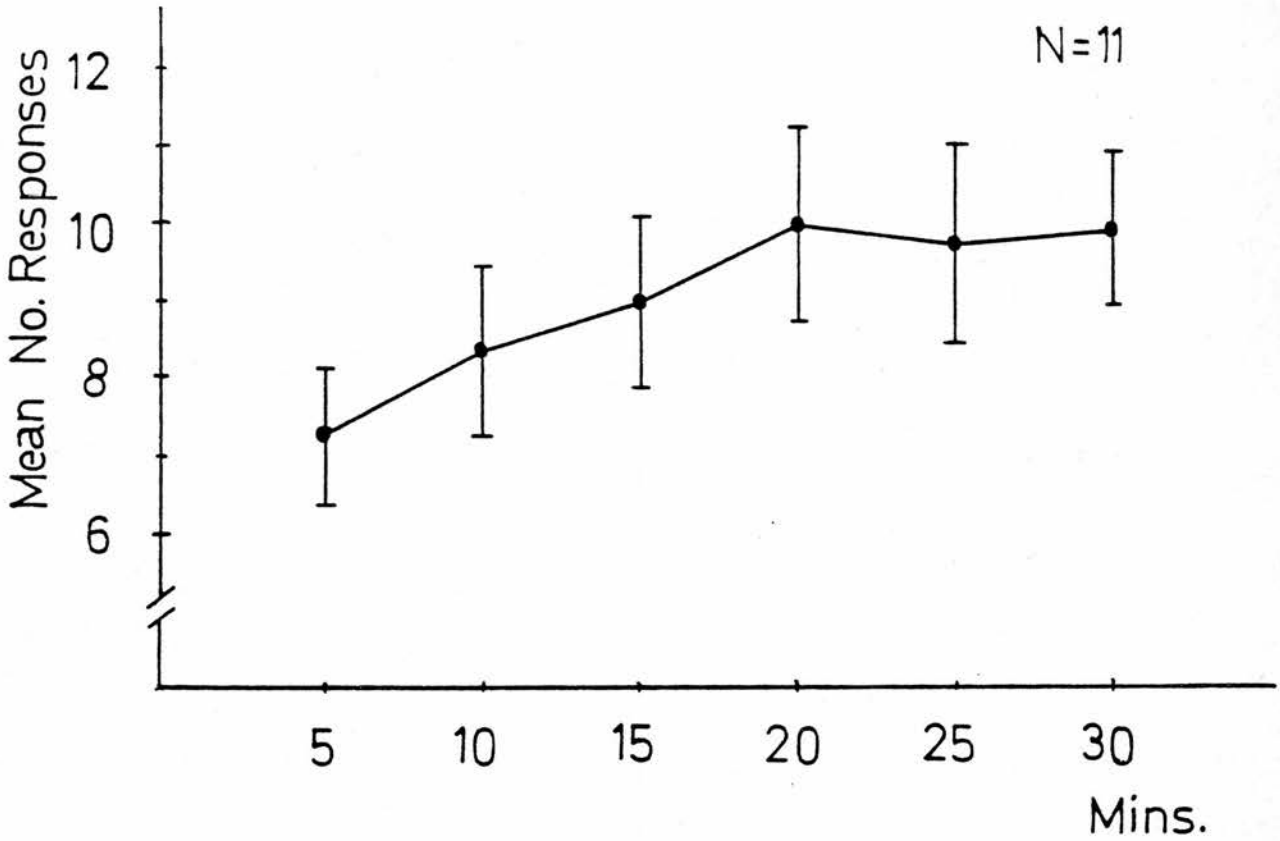
T = 1.5 N = 11 $p < .005$

Mean number of operant responses in successive 5 min. periods of:

A The first halves of sessions 2, 3, 4.

B The last halves of sessions 1, 2, 3.

	Chi	df	p
over all segments =	13.5844	5	$< .01$
over the first 3 segments (A) =	7.7727	2	$< .05$
over the last 3 segments (B) =	2.3636	2	N.S.


N=11
Mean No. Responses
12
10
8
6
5
10
15
20
25
30
Mins.

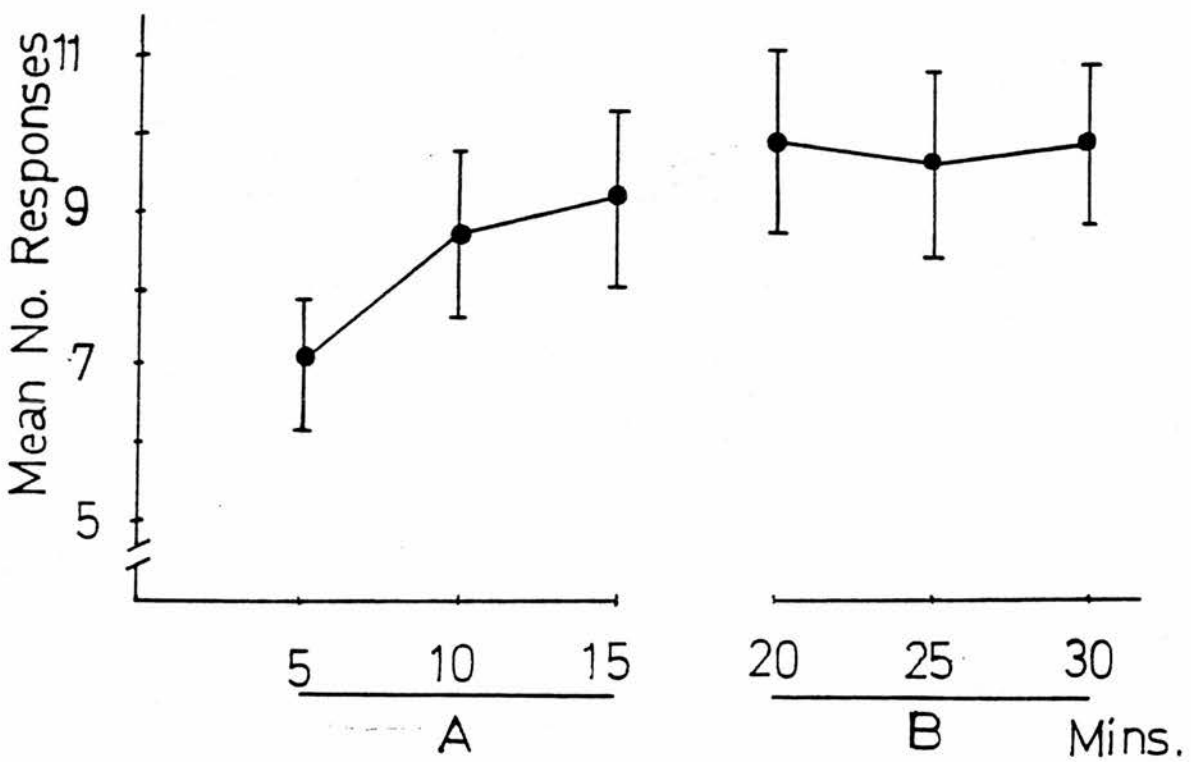

Mean No. Responses
11
9
7
5
5
10
15
20
25
30
A
B
Mins.

Table 12

The Spearmann correlations between mean biting (Bi), mean butting frequency (Bu(f)) and mean butting duration (Bu(d)) over successive minutes of testing (N =15).

Significance levels given are 1-tailed.

	Bu (f)	Bu(d)
Bi	.7841	.5550
Bu(f)		.7087

$p<.05$ denoted by _ _ _ _ _

$p<.01$ denoted by _____

Table 13

Comparison of the numbers of responses in the operant sessions termed "stable".

Significance testing by Friedman 2-way analysis of variance.

Session:	1	2	3	4
$\bar{X}$:	52.09	54.55	57.55	56.55
SEM:	6.09	5.88	6.44	7.25

Chi = 6.2454

df = 3

$p > .05$

CHAPTER 8

8.1 Operant Performance and the Parameters of Reward

An attempt to relate the aggressive displays elicited by reinforcement and the pattern of instrumental performance may be considered in some sense an investigation of the effect of "amount of reward". Some discussion of the findings of experiments concerned with the manipulation of reward amount is required. First, these effects will be considered when the reward is food or liquid. Following this, analogous experiments involving Betta splendens aggressive display will be discussed.

8.1 (a) Food and Liquid Rewards

Considering food and liquid rewards, many studies have investigated the effects of operant performance of the set of reinforcement parameters subsumed under the term "amount of reward". For food reward, Crespi (1944), Zeaman (1949), Logan (1960, p. 52-3) and Pubols (1960) showed that rats would run more quickly in a straight alley for large than for smaller quantities of food (for further references see Mackintosh, 1974). That reward magnitude effects operate in a manner similar to manipulations of motivational state (e.g. level of food deprivation) is suggested by Zeaman's (1949) finding that changes in amount of reward within an experiment produced an immediate shift in response latency in food rewarded rats.

For water reward generally similar results have been found. Rats run faster in straight alleys (Kintsh, 1962) and mazes (Wike and Farrow, 1962) for larger rewards. The reward magnitude effect in this case was on aquisition as well as asymptotic performance.

As Kling and Schrier (1971) have pointed out, there are several experimental manipulations which could be considered manipulations of reward amount. Quantity of reward material

duration of access to reward, size and number of food items and reward quality or preferedness could all be considered measures of the amount of reward, but may differ in their implications for operant performance. This is illustrated by Robbins' (1969) study in which rats were rewarded for running by being allowed to drink water from tubes of various diameters for various lengths of time. A positive correlation was found between running speed and the duration of access to water but not with the amount of reward actually consumed. The quality of a reward substance in terms of its "preferedness" can be measured outside the operant situation (see Young, 1945), and Guttman (1953) manipulated reward quality by using liquid rewards of differing sweetness (concentrations of sucrose solution). He found that rats increased their performance levels for sweeter rewards in terms of both rate of bar-pressing under periodic reinforcement and resistance to extinction. Similar findings are reported for alley running in rats (e.g. Goodrich, 1960, Kraeling, 1961, Knarr and Collier, 1962, Snyder, 1962).

When both quantity and quality of food reward for a bar-pressing response were manipulated by Hutt (1954) in a factorially designed experiment, both were found to have effect. However, all quantities used of the preferred (sweetenad) reward produced higher performance than all quantities of the basic food mixture which in turn produced higher levels of performance than all quantities of the least preferred (citric acid adulterated) food. Other early studies (mainly with rats) confirmed the findings described above consistently enough for Hilgard and Marquis (1961, p. 138) to be able to state that in general studies agree that,

> "...performance increases as a negatively accelerated function with increases in the amount of reinforcement".

More recent studies have led to the questioning of the generality of "amount of reward" effects. Lowe, Davey and Harzem (1974) found that the rate of responding of rats on a fixed interval schedule of reinforcement for rewards of

various milk concentrations did not vary. Furthermore, on fixed ratio schedules response rate was found to decrease with increases in concentration. In pigeons, responding on variable interval and variable ratio schedules, increases in the quantity of food reward produced no increase in operant response rate (Keesey and Kling, 1961; Neuringer, 1967), while Powell (1969) found that duration of the post-reinforcement pause in pigeons and fixed ratio schedules varied inversely with reward duration in contradiction to the findings of Lowe, Davey and Harzem (1974) for rats. Species differences in the effects of reward magnitude manipulations may therefore be of some importance.

Related to the reward magnitude effect is the phenomenon of negative contrast and in this species differences have also emerged. In rats, the reduction of reward magnitude within an experiment from "large" to "small" results in a level of performance for the "small" reward which is below that which occurs without preceding "large" rewards (Crespi, 1942). In target pressing goldfish, however, no such negative contrast occurs with food reward. If the amount of reward is increased, then performance level increases. If the amount of reward is then reduced, performance does not decline but remains at its former level (Lowes and Bitterman, 1967). Not only therefore does the relation between amount of reward and instrumental preformance depend on the way in which amount is manipulated, it also seems to vary with reward type and with species.

Some tentative explanations have been advanced to account for reward and species differences in reward magnitude effects. Hogan and Roper (1978) have suggested that the differences between milk and sucrose solutions in their effects on post-reinforcement pause may be attributable to differing metabolic responses to these. The difference between these rewards in their ability to produce a reward magnitude effect may be similarly caused. Kling and Schrier (1971) have proposed that sensory attractiveness may also be an important

factor. Whatever the source of reward and species differences in particular cases, an important conclusion which must be drawn from the very existence of such differences is, as argued earlier (ch. 1.7 (a)), that conventional food and liquid rewards are not homogeneous in their effects on operant performance.

For aggressive display reinforcement, as for conventional rewards, questions may be asked about the effects on performance of various parameters of reinforcement. When an operant response for display has been learned, is there any relation between the characteristics or the "amount" of reinforcement, and operant behaviour?

8.1 (b) Aggressive Display Reward

A basic question which must be asked about the control of instrumental behaviour by aggression reward is whether aggressive display is necessary at all for the stimulus to be rewarding. Johnson and Johnson (1973) showed that the opportunity to view a variety of stimuli (conspecifics, the subject's mirror image, a range of non-conspecifics, a coloured marble, or an empty chamber) reinforced a ring-swimming response equally well in terms of the rate of responding they produced. Although the subjects sometimes displayed initially during reinforcement by the various stimuli, display declined for all rewards over sessions, while operant responding continued. The authors conclude from this that the operant behaviour of Betta splendens may be motivated by curiosity as well as by aggression. However, Bols (1977) found that reward by presentation of a coloured marble would not support T-maze performance, and the findings suggesting that the level of performance supported by an aggression eliciting stimulus is related to its strength as an elicitor (see below) do not support the interpretation of Johnson and Johnson's results entirely in terms of curiosity.

Alternative explanations of Johnson and Johnson's (1973)

findings have been advanced. Hogan and Roper (1978) point out that interpretation of this experiment is difficult for two reasons. Firstly, the relative role of exploration in the reinforcement situation may be greater than usual in the very small (18 x 19 x 11 cms.) test chamber used. Secondly, the control period of no reward with which rewarded performance was compared was 20 hrs., as compared to 4 hr. experimental periods. Since Hogan (1961) has shown that automatically recorded attacks on a mirror during 24hr. periods of continuous illumination show a considerable diurnal variation, which may reflect a variation in general activity, comparison of time periods of different duration for any behaviour may be misleading.

Overall, the evidence suggests that although aggressive display may not be the sole source of motivation to respond for display reward, if large test chambers are used its role is far greater than that of exploration.

To what extent does the capacity of a stimulus to elicit aggressive display determine its effectiveness as a reinforcer for an instrumental response. Several investigators have applied themselves to this question concerning Betta splendens. Thompson in his (1963) demonstration of display reinforcement in Betta, compared the reinforcing effectiveness (in terms of rate of operant responding produced) of three reward stimuli which elicit aggressive display; the animal's own mirror image, a moving model of a male Betta in aggressive display and a similar stationary model. He found these stimuli to be reinforcing in decreasing order of effectiveness. Since Forselius (1957) has shown for Betta splendens that these stimuli elicit aggressive display in decreasing order of effectiveness, Thompson concludes that the reinforcing effectiveness of aggression eliciting stimuli is related to the efficacy of these stimuli in releasing aggressive display. Rhoad, Kalat and Klopfer (1975) confirmed Thompson's findings for mirror and models, also reporting that the sight of a live male Betta in aggressive display supports operant

responding at a higher rate than either miror image or models. From observations within their experimental situation, they confirmed that live males, mirror image, moving and stationary models elicit display in decreasing order of effectiveness. They did not, however, quantify the displays they observed in terms of frequencies and durations of the various display components, but instead report the occurrence ("maximally" or "some") of lateral display, the occurrence (or "some" occurrences) of biting and ramming, and the occurrence or non-occurrence of gill cover erection and display coloration.

Hogan and Bols (1980) investigated the relations between aggressive display in male Bettas and their performance in a runway for mirror image and live conspecific reward. They used two manipulations to investigate this relation. The first was based on differences between individual subjects in their readiness to display and the second involved the use of a priming procedure to manipulate aggressiveness in subjects just prior to testing.

In the first experiment, fish were divided into two groups before testing in the runway such that one group displayed strongly (over 85% of a 2min. test in frontal and lateral display) while the other group did not display to a conspecific at all. To control for differences in the general vigour of subjects, they were tested in a choice situation with food reward as well as displaying stimulus fish. Strong displayers chose food as often as did weak displayers, but chose the conspecific more often than weak displayers. This difference was not, however, statistically significant. Comparison of runway times for food in strong and weak displayers revealed no difference, but for display reward strong displayers swam significantly faster than weak displayers.

These results cannot be explained in terms of the occurrence of courtship behaviours, because the authors specifically state that "thrashing" did not occur in any

subjects. Interestingly, some stimulus fish did show this behaviour in response to weak displayers. From the difference in runway times for display between weak and strong displayers it must be the case that general level of aggressiveness determines runway performance for display reward.

In their first "priming" experiment, both duration of preexposure to a mirror image and the interval between trials were varied for strongly displaying fish. The effect of increasing priming was to decrease runway swimming times significantly. Because the different priming durations were used with different inter-trial intervals, the effects of these could not be separated. An additional experiment, in which reliably displaying fish were primed for "high" or "low" durations and tested in a food/stimulus fish choice situation (runway), revealed that high priming significantly increased the percentage of display choices. Low primed fish chose display at the same low level as before.

Hogan and Bols report that several measures of display behaviour were recorded, but for the last priming experiment only the effect of priming on gill cover erection in the runway was reported. Although the "high" priming group showed a higher level of mean gill cover than the "low" priming group, the difference was not significant. No data was presented concerning priming induced differences in reward elicited display while fish were in the goal box.

From all the experiments discussed above it would seem that the display which occurs during a reinforcement is to some degree related to the rate of operant responding such reinforcement maintains and that the inducement by priming of an aggressive state increased performance. Hinde (1970, p. 344) points out, however, that from experiments such as these, it is not possible to separate the reinforcing effects of the stimuli presented and the behaviours these stimuli elicit. That it may be the behaviours, rather than the stimuli per se, which determine operant response rate is suggested by Thompson (1963) and supported by the findings

of Bols (1977) who showed that for a T-maze situation, a complex stimulus which did not elicit display (a coloured marble) failed to sustain operant behaviour, while a live stimulus male which itself did not display but which elicited display in subjects, supported operant performance. A method by which the effect of the rewarding stimulus and the effect of the response it elicits might be separated will be suggested in a later chapter (ch. 11).

The experiments discussed above would seem to be more closely analogous to reinforcement "quality" experiments for food reward, although in none of these cases of display reward have preference tests been carried out as performed for food preference in rats (e.g. by Young, 1945). Analogous to studies varying the duration of access to food reward, is that of Hogan, Kleist and Hutchings (1970). For a ring swimming operant, the duration of mirror presentation reward was varied from 5 to 40 secs., and revealed no effect on response rate. Hogan and Roper (1978) cite an unpublished study by Grabowski and Thompson in which the duration of mirror-image rewards was varied from 15secs. to 150secs.. They found that the number of responses per session decreased as a function of reward duration. However, since the time occupied by reward during their 1hr. sessions was large, reconsideration by Hogan and Roper of these results in terms of response rate during the time available for responding (i.e. excluding reinforcement time) revealed that response rates for 60 and 100sec. presentations were greater than for 15-30sec. rewards. Whether Hogan et al. (1970) failed to find a reward duration effect because their maximum duration was only 40secs., or whether longer mirror presentations in their study failed to produce more aggressive display than their shorter presentations, is an open question.

In general, the usefulness of findings relating reinforcing effectiveness to the amount of aggressive display elicited is severely constrained by the failure of most investigators to adequately quantify display as it occurs in

their operant situations. Thompson (1963) did not observe reward-elicited behaviour, Hogan (1967) reports only the percentage time spent "displaying" in a test at the end of the experiment. Johnson and Johnson (1973) state only that their subjects

"...sometimes initiated partial or full threat displays..."

only observing aggressive behaviour more fully outside their operant situation, and to only some of their reinforcing stimuli. Rhoad, Kalat and Klopfer (1975) as previously mentioned only make a gross classification of displays (e.g. "some occurrences" of biting), while Hogan and Bols (1980) report gill cover erection durations in their runway but not during rewards.

To answer more fully the question of the relation between reward-elicited display and operant performance, an experiment is required which quantifies reward-elicited displays and relates these to subsequent operant behaviour. The use of reward stimuli which differ in their effectiveness as display elicitors or of fish which differ in their readiness to display would be ways of doing this. However, the reanalysis of data from Experiment 1 reported in ch. 7.2 indicated that natural variation in attack occurs within encounters. If these also occur in operant sessions over successive rewards, then these changes can be observed and related to the changes with have been shown to occur in operant behaivour.

Analysis of the results of the following experiment begins by attempting to relate the changes over operant sessions in reward-elicited attack with changes occurring in operant behaviour. This is followed by an investigation of the relations between other reward-elicited behaviours and operant responding, in terms of both their temporal patterning within sessions and inter-subject variation.

8.2 The Relations Between Reward-Elicited and Post-Reward Behaviour and Operant Performance - Experiment 6

8.2 (a) Behaviour During Operant Sessions for Display Reward - A Qualitative Description

Before listing categories of behaviour used to describe reward-elicited and other behaviours which occur in the operant situation, a qualitative description of these may be useful.

An operant session of 30mins duration begins with the subject performing the first operant response. When the subject leaves the response gate the stimulus cover is raised to expose the stimulus male. Even before the cover is raised sufficiently for visual contact between subject and stimulus to be established, the subject approaches the rising stimulus cover with its gill covers erect. By the time visual contact is possible the subject will usually be within one fish length of the stimulus in a frontal display (FD). The stimulus fish will then turn to lateral display (LD). During the 30secs. for which the stimulus cover is fully raised, subject and stimulus fish will continue to cycle through frontal and lateral displays, some lateral displays being followed by protracted air gulps (AG). Both LD and AG are sometimes accompanied by tail beats (TB). When the stimulus cover descends after 30secs., thus terminating the reinforcement presentation, subject and stimulus fish often swim downwards with it, maintaining visual contact for as long as possible. Stimulus presentations may therefore exceed 30secs. by the one or two seconds which it takes for the stimulus cover to reach its maximum elevation and return from this maximum to the level of the tank substrate. The level at which the stimulus fish is inside its container when the cover is raised allows this variability when ths stimulus is first presented, while the extent to which fish follow each other down the height of the stimulus container is the determinant

of variability in the time at which stimulus presentation terminates.

After reinforcement fish were never observed to swim directly from the reinforcement site to the response gate and there perform an operant response. Instead fish would swim in a circular way around the stimulus container in a series of short bursts. Often the direction of circling would change. During swimming bursts the medial fins would be close to the body and the pelvic fins held horizontal to the substrate and parallel to the longer axis of the body. Such bursts of swimming are followed by short periods during which the fish is stationary with its medial fins partially or fully raised and its pelvic fins dropped vertically towards the substrate. The erection of the medial fins and the lowering of the pelvic fins are simultaneous actions. After a period of such swimming the subject will leave the reinforcement site (i.e. move away from the stimulus cover to a distance greater than one fish length) either directly towards the response gate or towards the walls of tha tank. If the movement is in the former direction then it may not be followed immediately by an operant response. Often the fish will stop and turn around through an angle of 180° in a single movement and move back towards the reinforcement site. Such reversals in orientation may occur several times and may be followed by more swimming around the stimulus container or by an operant response.

If the subject leaves the reward site swimming in a direction other than towards the response gate it is very likely to swim up and down the tank walls in a way very similar to the behaviour described as wall swimming (Wls) in ch. 4.2 which occurred during presentations of a female, or male subordinate, when subjects were in nest building condition. The difference in this situation is that wall swimming never occurs during stimulus presentations, only between reinforcement termination and the subsequent operant response. In addition,

it is generally a good deal less vigorous but can account for a considerable proportion of the interval between reward termination and the operant response. Wall swimming may be followed by a return to the reward site (circling with bursts of swimming always occurs during such returns) or by movement from the tank wall to the response gate.

While observing these behaviours a vivid impression is gained of a conflict between the tendency to stay in the region in which the conspecific stimulus was last seen and the tendency to leave that site and perform the behaviour leading to a further period of visual contact with the "intruding" male, i.e. the operant response. Indeed in the wild, periods of visual contact with an intruder might occur and be broken off not only by the retreat of the intruder but by the loss of visual contact due to dense vegetation interposing itself between the combatants. If such a situation arose with any frequency a "search strategy" might well have evolved which includes a period of intensified swimming interspersed with a visually striking display (medial fins erect), which would increase the probability of the combatants regaining contact to continue and resolve the dispute. Such a strategy might be expected to include a period of swimming about quite close to the place at which the intruder was last seen, only expanding the area of "search" later. Why such a strategy (if it were shown to exist) might evolve at all is an interesting question and the answer may lie in the investment of time and energy made by combatants in a dispute which has not been settled.

Apart from such speculation about the functions of elevated swimming rates after interupted aggressive encounters and the spatial distribution of such swimming, it seems a plausible suggestion that some motivational incompatibility may occur when Betta splendens is required to leave the site of a conspecific presentation in order to earn a further presentation. It may be that these post-reward motivational states may be an important limitation on the

rate of operant responding for aggressive display reward in this species and the following experiment will include the observation and quantification of some aspects of post-reward behaviour.

8.2 (b) Recording Apparatus

The WRATS behaviour recording apparatus used for experiments 1 - 4 and described in section 4.1 was used to record the behaviours performed by subjects and stimulus fish during operant sessions. A simple modification to the WRATS keyboard was carried out to enable automatic recording of the occurrence of operant responses and the presentation of rewards. Responses were automatically recorded as momentary key depressions while reinforcment presentations were represented by a key depression lasting from reward initiation to termination.

8.2 (c) Behaviours Recorded

All the behaviours listed in ch. 4.2 were recorded with five additions and with the criterion for withdrawal (Wi) altered.

Operant response (Op): The occurrence of an operant response automatically closes a switch on the WRATS keyboard momentarily.

Reinforcment presentation (Rf Pr): The onset of a reward presentation automatically closes a switch on the WRATS keyboard which remains closed (equivelant to a key depression) for the duration of the presentation. This allows computer programmes used for analysis of WRATS output to identify stimulus presentations independently of the behaviours which occur during these presentations. A distinction can therefore be made between events occurring during reward and the same behaviour occurring between rewards.

Visual contact (VC): Since the initiation of a stimulus presentation by raising the stimulus cover may not immediately expose the stimulus to the subject, and since the time of termination of a presentation depends on the level at which the subject and stimulus fish are swimming, some more exact

estimate of reward duration is necessary. To get such an estimate the experimenter estimates visually the point in the upwards journey of the stimulus cover at which subject and stimulus fish come into visual contact. This is recorded by the momentary depression of the VC key.

End of visual contact (EVC): This key is depressed when the experimenter considers visual contact between subject and stimulus fish to have been terminated by the downward movement of the stimulus cover.

Search swim (SeS)*: After a stimulus presentation ends, subjects will swim in a circular movement around the (now lowered) stimulus cover, remaining within one fish length of it. This swimming is performed by rapid beating of the pectoral and caudal fins while the medial and pelvic fins are flat against the body surface.

Search with dorsal fins erect (SeD)*: The swimming bouts named "search swimming" above are punctuated by periods in which the fish is stationary with partially or fully erect medial fins and lowered pelvic fins.

Swimming from reward site to response gate (Rf - Op): After reward termination fish may swim directly towards the response gate. If such swimming involves moving one fish length away from the reward site then the Rf - Op key is momentarily depressed.

Swimming from response gate to reward site (Op - Rf): On arriving within one fish length of the response gate from any part of the tank subjects may swim directly towards the reward site and arrive within one fish length of it. If this occurs the Op - Rf key is momentarily depressed.

Withdrawal (Wi): In the earlier experiments a withdrawal was defined as a movement of the subject which took it away from the stimulus cover a distance in excess of one fish

*The term "search" as used here is not intended to have any implications concerning the behaviours actual causation or function. It merely refers to the rather striking impression of "appetitiveness" gained by observers.

length in any direction. For this and subsequent experiments the definition of a withdrawal is altered to exclude movements in the direction covered by Rf -Op. A withdrawal is a movement away from the reward site but not directly towards the response gate. In practice Wi and Rf - Op are easily distinguished.

Several measures of the above behaviours and those described earlier (ch 4.2) were used. with the exception of biting (Bi), tail beating (TB), swimming from response gate to reward site (Op - Rf) and from reward site to response gate (Rf - Op), which behaviours are measured in terms of frequency only, the durations of behaviours were recorded as well as their frequencies. When a behaviour is named, the measure in question will be indicated by a single letter in parethesis (d, for duration; f, for frequency) appended to the behaviour name abbreviation.. This FD(d) refers to frontal display duration and SeS(f) refers to search swim frequency.

8.2 (d) Experimental Method

On the day following the four consecutive stable sessions described in the previous experiment (ch. 7.3 (c)) all 11 subjects had one more session of operant conditioning. The procedure followed in this experiment was identical to that for the previous experiment except for the observation and recording of the behaviour of subjects and reinforcing stimulus fish. Operant sessions were not necessarily observed in their entirety, but the first and last 16 consecutive reinforcements were observed for every subject. If a session longer than 30mins. (exclusive of reward time) is necessary for a subject to earn 32 rewards then the session was continued until this had occurred. It is important to point out that the 30 rewards and post-reward intervals used as the basis for data analysis in this experiment represented consecutive reinforcements only for the first and last rewards for many subjects.

8.2 (e) Changes in Attack and Operant Responding Over Sessions- Method of Analysis

To confirm that operant response rate increases during observation sessions and to attempt to detect a concomitant increase in attack behaviours, the units of analysis taken are the reward and the latency to the response following that reward (operant response latency). For each subject, therefore, the description of its behaviour was in terms of the behaviours occurring during successive rewards and post-reward intervals. Only the first and last 15 rewards and operant latencies were used in analysis.

To test the significance of changes occurring in operant response latency and biting over sessions, the mean over subjects of these variables was taken for each successive reward and post-reward interval, and correlated with the serial order of the observation (1-30). Spearman's rank correlation was used and significance testing was 1 - tailed. In addition it was hypothesised that:

a) The mean operant response latency for the first 5 rewards would be greater than for the last 5 rewards.
b) The mean number of bites occurring in the first 5 rewards would be less than for the last 5 rewards.

Significance testing was by Wilcoxon matched pairs signed-ranks test (1 - tailed).

8.2 (f) Results

Data from 3 of the 11 subjects had to be discarded due to data corruption by a computer paper tape punch fault. For the remaining subjects Fig. 23 shows that the mean latency of the operant response decreased over the 30 responses observed. The correlation between mean operant response latency and the seial order of the observations was - .6406 (Spear., $p<.01$, 1 - tailed). The difference between the

mean latency to responses after the first 5 rewards and the mean latency to responses after the last 5 rewards is significant (Wilcx., $p<.05$, 1- tailed), and shown in Fig. 24. The hypothesis that the mean number of bites per reinforcement would also increase into the session was also supported. Fig. 23 also shows that the mean number of bites increased significantly, with the correlation between the mean number of bites per reinforcement and the serial order of the observations at .8410 (Spear., $p<.01$, 1 - tailed). The difference in mean number of bites elicited by the first and last rewards observed (Fig. 24.) is significant (Wilcoxon, $p<.025$, 1 - tailed).

8.2 (g) Discussion

The mean number of bites which occurred in the present experiment was less than expected. In Experiment 1, rivals were presented for 15mins., which is an equivalent time period to that observed in the operant situation (30 x 30sec. rewards). However, the mean number of bites for the first rival session was 14.43, while for the operant session it was only 8.11 bites per subject. Although such a cross experiment comparison is of no value as evidence, it does suggest that intermittent stimulation may have less effect of increasing attack than continuous stimulation. This possibility will be investigated fully in a later experiment. (ch. 10)

The previous analysis confirmed that operant latency decreases into sessions and showed that biting increases into those sessions. This supports the hypothesis that the attack tendency is involved in the motivation of operant responding for display reward. It must be noted, however, that the decrease in operant latency and the increase in biting are not contemporaneous, in that biting increases after the sharpest decrease in operant latency has already taken place. If attack is involved in determining operant

latencies, then subthreshold increases in the attack tendency may be sufficient to produce a detectable decrease in operant latency.

As well as a motivational link between attack tendencies and operant behaviour, there is the possibility that other behaviours related or unrelated to attack may be involved. The following analyses examine the relations between reward elicited behaviours and each other, and following this, their relations with operant responding.

8.3 The Relations Between Reward-Elicited Behaviours

The previous analysis showed that as attack increased, the latencies to operant responses decreased. Since these changes were not simultaneous, the possibility was raised that levels of the attack tendency subthreshold for overt attack might be involved in determining operant latency. Although attacks did not occur until several reinforcements into operant sessions, display always occurred during rewards and was recorded. It is possible that some of these displays are caused by or inhibited by the system that underlies attack. If the relations between all recorded reward-elicited behaviours were determined, than it could be predicted that all those positively related to attack would be negatively related to operant latency, while those negatively related to attack would be positively related to operant latency.

The following analysis examines the relations between reward-elicited behaviours.

8.3 (a) Method of Analysis

Durations and frequencies of each behaviour were computed for each observed reward and correlated with the durations and frequencies of every other behaviour. The

correlations procedure used in the following analysis was Spearman's rank order correlation coefficient (Siegal, 1956, p.202). A problem which must be considered concerns the interpretation of correlations obtained. Since the Spearman correlation procedure involves the ranking of scores on the variables to be correlated, the lumping together of data from different subjects with differing levels of these behaviours might give misleading results. Nevertheless, the large number of degrees of freedom which such a procedure involves allows the detection of much weaker relations than would be discovered otherwise. Therefore, one method of analysis used was the correlation of reinforcement elicited behaviours with each other over each of the 30 rewards observed and data from subjects was pooled (N = 270). This will be referred to as method "PCor". (pooled for correlation).

The second method used involved the generation of a "mean subject". That is the 30 rewards and post-reward intervals observed were numbered according to the serial order of the observation from 1 - 30. Post-reward interval 1 therefore follows reward 1 which is in turn followed by reward 2. For each serial order position, (e.g. reward 3) the mean of each measure (frequency, duration) of each behaviour was calculated across subjects. Correlations were then performed on the mean (across subjects) amount of a behaviour shown (e.g.mean bites during reward 3) and the mean amount of other behaviours (e.g. the mean duration of LD during reward 3). Inspection of the data revealed that the mean was appropriate as a measure of behaviours since the results of ranking procedures applied to a set of means generally agreed well with the results of ranking procedures applied to the set of medians derived from the same data. This method of correlating the over session means of behaviours will be referred to as method "MCor" and N = 30. One difficulty for the interpretation of the results of both this method and the previous method using pooled data (PCor), is that if 2 measures of reward-elicited behaviour are found to be

significantly correlated, the correlation may be due, not to a causal relation between the variables but to the presence of simultaneous trends in these variables over the operant session. That is, the correlation between these variables may be due to their independent correlation with a third variable, i.e. the serial order of the observation. Ideally, the effect of such a third variable could be isolated by the use of a partial correlation procedure (see Guilford 1973, p. 312) but in the present case a nonparametric correlation procedure must be used (the change in the variance of variables such as biting over sessions for example is fairly large and it is far from certain that the assumptions on which ~~non~~parametric correlation procedures are based are fully satisfied). Since the sampling distributions of the nonparametric partial correlations suitable (e.g. Kendall's) are not known, the usefulness of nonparametric partial correlation is limited and this method will not be used here. Some control of trends across sessions is nevertheless required so a third Spearman correlation procedure was applied, which exploits the differences between individuals. This method involves the calculation of mean amounts of behaviours per reward for entire sessions for each subject, and the correlation was performed on those means over subjects (N = 9). With N = 9 a high correlation is needed in order to reach significance, but the sign of correlation will be a useful indicator as to the likelihood of the correlations resulting from the previous methods (PCor and MCor) being attributable to simultaneous but independent trends. The method of correlating across subjects will be referred to as method "SCor".

8.3 (b) The Criterion for a Significant Relation

The use of three different correlation methods leaves the problem of deciding on a criterion for taking a correlation to have been demonstrated. It must be said that this choice

of criterion is unavoidably a rather arbitrary procedure. A correlation will be considered to have been adequately demonstrated if all three methods produce correlation coefficients of the same sign and if one of these correlations is significant. All correlation coefficients generated by all methods will, however, be reported. When this criterion has been satisfied, this will be indicated in discussion by appending an asterisk to the term "relation". Thus, "a positive relation* was shown to exist between A and B" would mean "the correlations between A and B were positive by methods MCor, PCor and SCor and one of these was significant.

8.3 (c) Results

Table 14 gives the results of the intercorrelation of reward elicited behaviours by the three methods used. The testing of the significance of these correlations was 2 - tailed. Because of this, the methods with small numbers of observations (MCor and SCor) could only be tested for significance at the .02 level, since tables of critical values for small samples are 1 - tailed. The critical value of rho at the .05 level of significance for method PCor (N = 270) was calculated by the method suggested by Guilford (1973, p. 284).

Fig. 25 is a diagrammatic representation of the relations* between reward-elicited behaviours. It can be seen from this that the attack behaviours Bi, Bu(f) and Bu(d) are positively related*. The relations* between the behaviours AG(f), AG(d), TB, FD(f) and FD(d) and the relations* between these and biting and butting are positive. Only the single behaviour LD(d) is negatively related* to any other behaviours and these behaviours are the overt attack measures Bi, Bu(f) and Bu(d).

The behaviours discussed may be divided into two groups. In the first group are those which, if they are related* to attack at all, the relations* are positive. Relations* between members of this group are never negative. The second group

includes only the behaviour LD(d), which is negatively related* to attack measures, and is not positively related to any behaviour of the first group.

8.3 (d) Discussion

Two groups of behaviours have been identified. The behaviours of the first group are never negatively related* to each other and many are positively related* to biting and butting (all measures). This group will be termed the "attack group", not because all behaviours in the group are positively related to attack (they are not) but because the attack behaviours biting and butting occur in it. The second group containing only LD(d) is negatively related* to some behaviours of thd attack group and will be termed specifically LD(d).

It has already been shown that increases in operant response rate occur into operant sessions. It has also been shown that the rate of biting reward increases into sessions. If the motivational system controlling attack behaviours is involved in the motivation of operant responding then it would be expected that negative correlations would be found between attack behaviours occurring during rewards and the latency to the operant response following those rewards. If the attack tendency motivates operant responding, then a behaviour negatively related* to attack (LD(d)) would be expected either to inhibit operant responding or to indicate a low level of the attack tendency. In either case, a positive correlation would be expected between LD(d) and operant latency.

Considering other reward-elicited displays, some of these have been shown to be positively related* to some attack behaviours and none are negatively related* to these. It can be hypothesised that these displays are caused by tendencies linked with the attack tendency and it would be expected that they would be, like attack behaviours, negatively

correlated with latencies to the operant response. The following analysis investigated the relations*between reward-elicited behaviours and operant responding.

8.4 The Relations Between Reward - Elicited Behaviours and Operant Responding

8.4 (a) Introduction

On the basis of the relations* between the different reward-elicited behaviours, the following predictions were made about the relations* between these and operant latency.

1. Bi, Bu(f), Bu(d), AG(f), AG(d), TB, LD(f), FD(f) and FD(d) will be negatively related* to operant response latency.
2. LD(d) will be positively related* to operant response latency.

8.4 (b) Method of Analysis

The behavioural data used in the previous analysis and operant response data from those same sessions were further analysed. As before, the first and last 15 rewards observed provided display data for each subject. Each of these rewards (1-30) was followed by a latency to the next operant response. These can also be numbered in the order that they occurred, from 1 - 30. Thus, ignoring the first response (which initiated sessions) and beginning with the first reward, 30 reward/operant latency pairs occurred for each subject, such that reward 1 was followed by operant latency 1 and so on, until reward 30 was followed by operant latency 30. Within sessions therefore, events occurring during rewards can be correlated with the latencies to the operant response following each of those rewards.

The correlation methods MCor, PCor and SCor were used in this analysis as in the last. For method MCor, the means

over subjects of each behaviour of the 30 rewards was correlated with the means over subjects for each of the 30 operant latencies (N=30). For method PCor, data was pooled with each of the 9 subjects contributing 30 reward-operant response latency pairs for correlation (N=270). For method SCor, each reward-elicited behaviour over the 30 rewards observed was experssed as a mean value for each subject and was correlated over subjects with each individual's mean operant latency (N=9). The criterion for the demonstration of a significant relation between variables was the same as for the previous analysis and similarly denoted (relation*).

8.4 (c) Results

Table 15 shows the sizes and levels of significance (1 - tailed) of correlations between amounts of reward-elicited behaviours and the latency to the operant response, for the three correlation methods used. Fig. 26 shows a diagrammatic representation of the relations* between operant latency and reward-elicited behaviours. In addition, the relations are shown between these reward behaviours as revealed by the previous analysis. All attack behaviours, (Bi, Bu(f) and Bu(d)) and air gulp frequency AG(f) are negatively related* to the operant latency (Op.Lat.), while lateral display duration (LD(d)) is positively related to operant latency. The criterion for the existence of a relation* requires that although all three methods should produce correlations of the same sign, only one need be significant. For all the relations* found in this analysis, however, at least two correlation methods gave a significant result.

8.4 (d) Discussion

Several of the group of behaviours termed the attack group in the previous analysis have been shown to be negatively related* to operant response latency. In addition, LD(d),

which was negatively related* to behaviours of the attack group, has been shown to be positively related* to operant latency.

It should be noted that not all of the behaviours placed in the attack group were negatively related* to operant latency as was hypothesised. In the attack group, the only behaviours positively related* to an overt attack behaviour were AG(f) and TB. AG(f), like attack behaviours, was found to be negatively related* to operant latency, but TB was not. It seems from this that for a reward-elicited behaviour to be negatively related* to operant latency, it must be positively related* to overt attack. The case of TB, however, seems to indicate that a positive relation* with overt attack may not be sufficient to produce a negative relation* between the behaviour and operant latency.

The present analysis has shown that reinforcement-elicited behaviours differed with respect to their relations with operant responding, and that the few display behaviours which were negatively related* to operant response latency were found to be positively related* to overt attack in the previous analysis. In addition, the single display behaviour found to be positively related* to operant response latency was negatively related* to overt attack. The explanation of these findings might demand that two motivational systems be considered, one of them (an attack or aggression system) facilitatory towards the tendency to perform the operant response, while the second system underlying lateral display duration is inhibitory towards operant behaviour. It must be pointed out, however, that from the data available, it cannot be concluded that lateral display represents the activity of a "fear system". The finding of a negative correlation between behaviours does not necessarily imply that the systems underlying those behaviours are in any way conceptually opposite (e.g. fleeing/freezing). Rather different kinds of evidence would be required to demonstrate control of lateral display by fear (e.g. a positive correlation

with the size of the rival). The finding of negative relations* between e.g. biting and lateral display duration may simply mean that a single process is at work, which controls the relative levels of the two behaviours, such that as the value of a single motivational variable increases, one of the behaviours increases while the other decreases. The negative relation* between LD(d) and operant latency may therefore mean that LD(d) indicates a low level of a single operant- controlling tendency. i.e. attack.

In ch. 7.3(f), the distribution of inter-response intervals was examined and it was noted that few IRI's of less than 10secs. occurred even though this was ample time for performance of the operant response. In ch. 8.2(a), a qualitative description of behaviour during operant sessions was given and it was suggested that behaviours occurring after rewards (during operant latencies) might inhibit performance of the operant response. The following chapter investigates the relations* post-reward behaviours, and the relations* between these and operant latency. In addition, the possibility will be considered that the effects of reward-elicited behaviours on operant responding are not direct but instead mediated by their effects on post-reward behaviours.

Figure 23

The change in mean operant latency (Op. Lat.) and mean biting frequency (Bi) over the 30 rewards and operant latencies observed. Reward events at a particular observation serial position (1 - 30) immediately precede the operant latency at that serial position. N = 9.

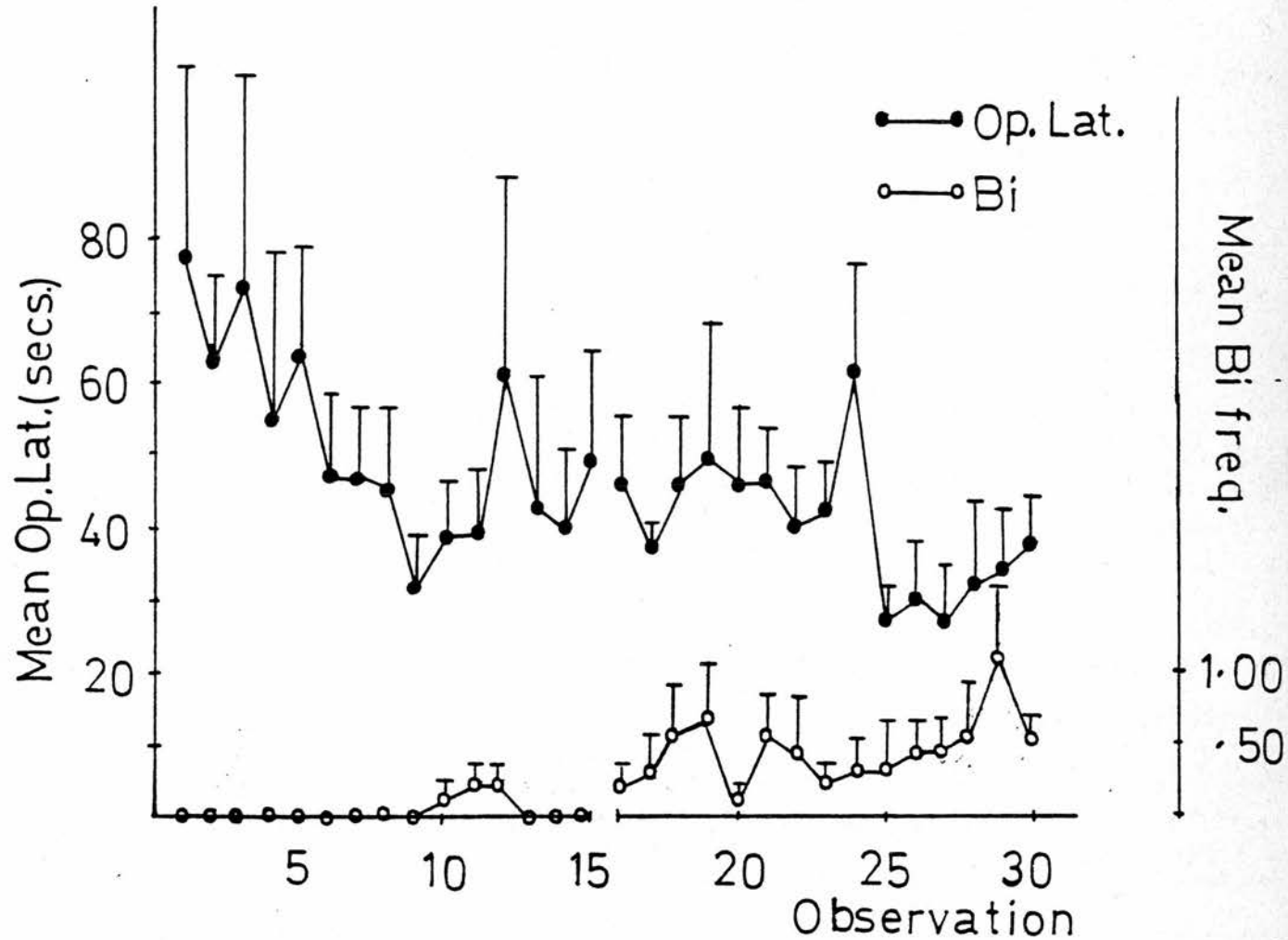
Spearman correlations (1-tailed)
with observation serial position.

Op.Lat.	rho =	-.6406
	df =	28
	p <	.01
Bi	rho =	.8410
	df =	28
	p <	.01

Figure 24

Mean operant latency and bites per reinforcement during the first 5 (F5) and last 5 (L5) observations of the test. Significance testing by Wilcoxon test (1-tailed).

Op.Lat. :	T = 7	N = 9	p<.05
Bi :	T = 0	N = 6	p<.025


Op. Lat.
Bi
Mean Op.Lat.(secs.)
80
60
40
20
Mean Bi freq.
1·00
·50
5
10
15
20
25
30
Observation

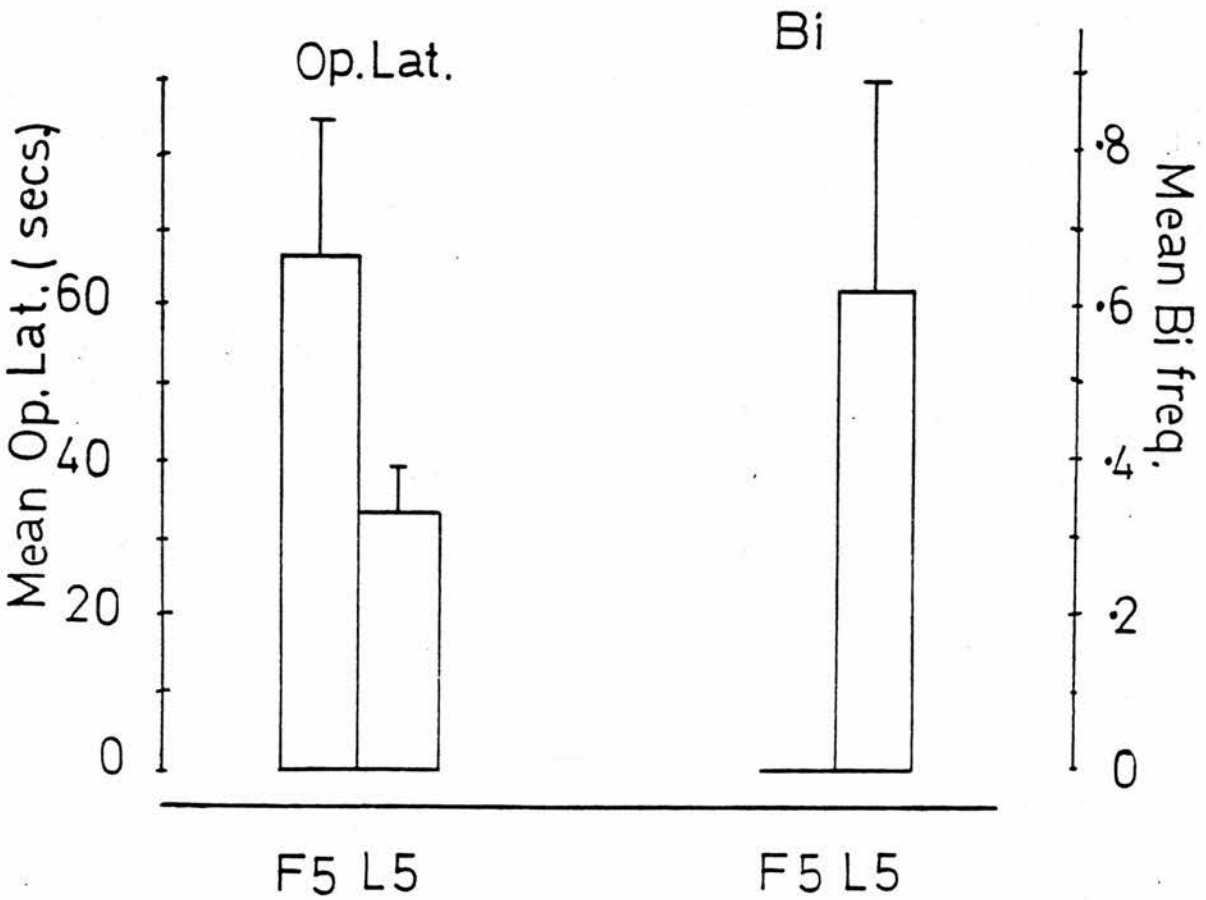

Op.Lat.
Bi
Mean Op. Lat.(secs.)
60
40
20
0
Mean Bi freq.
·8
·6
·4
·2
0
F5 L5
F5 L5

Figure 25

The relations* between reward-elicited behaviours.

Positive relation* denoted by _____

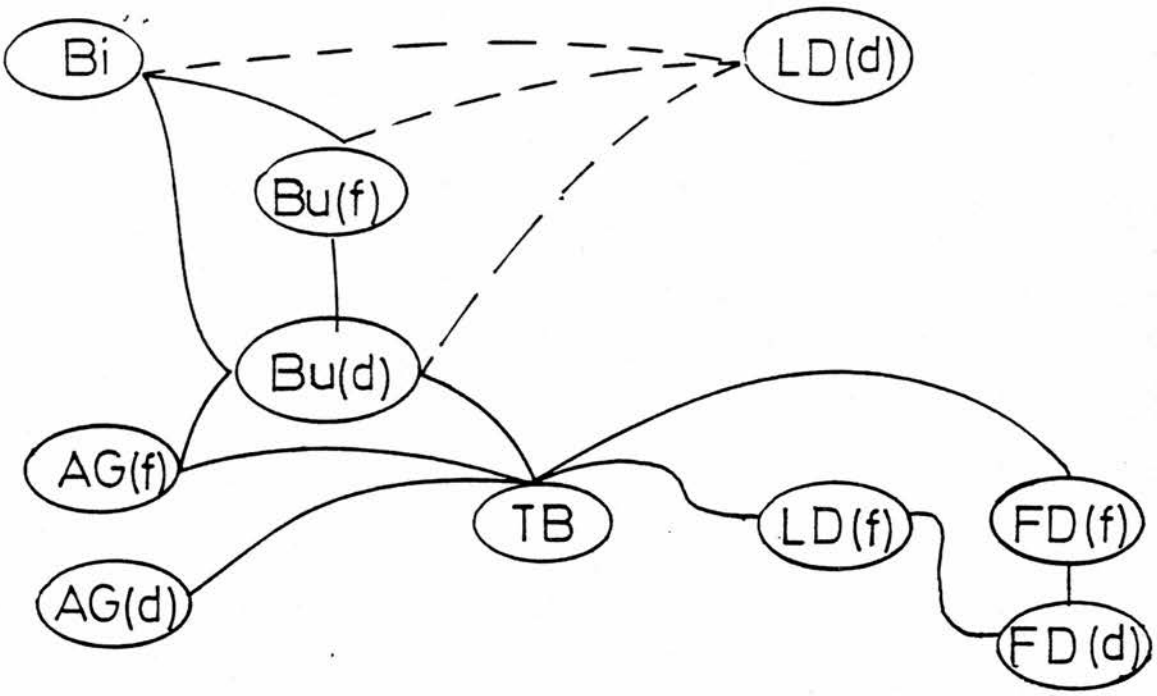
Negative relation* denoted by _ _ _ _

Figure 26

The relations* between reward-elicited behaviours and operant latency and the relations* between those reward-elicited behaviours.

Positive relation* denoted by _____

Negative relation* denoted by _ _ _ _


Bi
LD(d)
Bu(f)
Bu(d)
AG(f)
TB
LD(f)
FD(f)
AG(d)
FD(d)

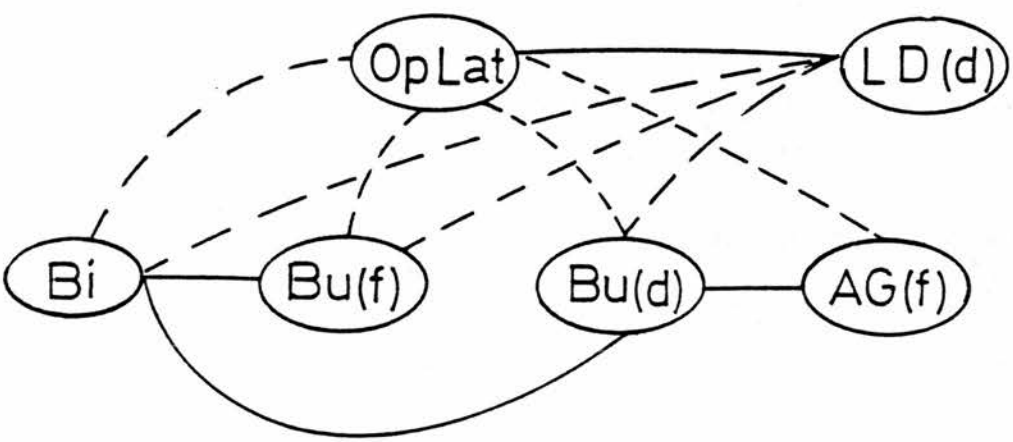

OpLat
LD(d)
Bi
Bu(f)
Bu(d)
AG(f)

Table 14

The Spearman correlations between reward-elicited behaviours.

Significance levels given are 2-tailed.

	TB	Bu(f)	Bu(d)	FD(f)	FD(d)	LD(f)	LD(d)	AG(f)	AG(d)	Method
	.652	.833	.830	.492	.457	.270	-.426	.345	.368	MCor
Bi	-.105	.600	.588	.207	.254	.133	.159	.054	-.023	PCor
	-.135	.870	.786	-.259	-.418	-.352	-.469	.265	-.335	SCor
		.530	.601	.328	.313	.185	-.312	.420	.322	MCor
TB		.046	.045	.458	-.218	.412	.244	.520	.444	PCor
		-.290	.059	.561	.259	.502	.536	-.403	.653	SCor
			.839	.488	.450	.335	-.465	.350	.441	MCor
Bu(f)			.998	.204	.232	.070	-.207	.030	.017	PCor
			.815	-.343	-.343	-.586	-.435	.374	-.326	SCor
				.442	.388	.278	-.475	.472	.564	MCor
Bu(d)				.197	.232	.063	-.211	.033	-.013	PCor
				-.034	-.335	-.360	-.360	.370	-.193	SCor
					.601	.891	-.361	.564	.242	MCor
FD(f)					.235	.883	.283	.338	.087	PCor
					.733	.433	.733	-.619	.683	SCor
						.474	-.476	.442	.147	MCor
FD(d)						.112	-.266	-.155	-.298	PCor
						-.050	.917	-.879	.800	SCor
							-.096	.433	.114	MCor
LD(f)							.407	.392	.108	PCor
							.133	-.042	.117	SCor
								-.532	-.414	MCor
LD(d)								.006	-.181	PCor
								-.862	.817	SCor
									.613	MCor
AG(f)									.802	PCor
									-.837	SCor

			Indicated by
MCor:	N = 30	$p < .02$	———
PCor:	N = 270	$p < .05$	- - - - -
SCor:	N = 9	$p < .02$	———

Table 15

The Spearman correlations between operant latency and reward-elicited behaviours. Significances given are 1-tailed.

	Bi	TB	Bu(f)	Bu(d)	FD(f)	FD(d)	Method	N
	-.435	-.351	-.467	-.490	-.387	-.358	MCor	30
Op.Lat.	-.234	-.239	-.194	-.185	-.103	-.098	PCor	270
	-.661	.594	-.753	-.293	.433	.267	SCor	9

	LD(f)	LD(d)	AG(f)	AG(d)	Method	N
	-.299	.395	-.451	-.411	MCor	30
Op.Lat.	-.011	.236	-.167	-.180	PCor	270
	.383	.417	-.251	.433	SCor	9

	indicated by
$p < .05$	- - - - -
$p < .01$	———

CHAPTER 9

9.1 The Relations Between Post-Reward Behaviours

9.1 (a) Introduction

It is being suggested that post-reward behaviours do not simply occupy the time during which the motivation to perform operant responses is low, but actually inhibit operant responding. It may be useful to describe these post-reward behaviours again.

The end of each reinforcement is followed by a period of swimming in a circular motion around and close to the reward stimulus cover. These behaviours were called "search swim" (SeS) and "search stop with dorsal fins erect" (SeD). After a period of such swimming, subjects may swim away from the reward site either directly towards the response gate (Rf - Op) or in another direction (Wi). After arrival at the response gate, fish sometimes swim directly back towards the reward site (Op - Rf) and perform more SeS and SeD. This "vacillation" might involve several trips back and forth between the reward site and the response gate, without the operant response actually being performed. After leaving the reward site or the response gate and before an operant response is performed, fish would sometimes swim up and down the tank walls (Wls).

The following two analyses will attempt to discover:

1. The relations* between post-reward behaviours.
2. The relations* between these behaviours and operant latency.
3. The relations* between reward-elicited and post-reward behaviours.

9.1 (b) Method of Analysis

Since it has been hypothesised that those behaviours which occur during the post-reward interval are not merely occupying the time during which the subject is insufficiently

motivated to perform the operant response, but instead actively inhibit the response, it is not sufficient to show that the absolute amounts of post-reward behaviours are correlated positively with the latency to the operant response. It is also necessary to show that the rate of performance of post-reward behaviours, or the proportion of the operant latency they occupy, is positively correlated with the operant latency. Whenever frequencies or durations of a behaviour have been expressed in terms of the operant latency, they will be referred to as "rates" of performance of that behaviour.

The data on which the following analysis is based were collected from the same sessions as were data concerning reward-elicited behaviours and operant latencies. The correlation method was Spearman's rank correlation and the three correlation procedures MCor, PCor and SCor were used as before. The criterion for the demonstration of a relation* as described in 8.3(c) remained unchanged. In the analysis of the relations* between post-reward behaviours, significance testing of correlations was 2 - tailed.

9.1 (c) Results

Table 16 shows the Spearman correlation coefficients for the intercorrelation of the rates of post-reward behaviours. The relations* between these were as schematically represented in Fig. 27. It can be seen that post-reward behaviours are roughly divisible into two groups. The first such group consists of SeS(f), SeD(f), SeS(d), SeD(d) and Rf - Op. The second consists of the behaviours Wls(d), Wls(f), Wi, Ap and Op-Rf . Relations* across groups were in every case negative while relations* between members of a group were positive.

9.1 (d) Discussion

Post-reward behaviours were roughly divisible into two groups. In the first group were the behaviours which occurred

immediately after reward termination and which occur in close proximity to the reward site. Search swimming and search with dorsal fins erect were, for the most part, positively related* in both their frequency and duration measures. Also related to these was the movement from reward site to operandum, although it is interesting to note that this latter behaviour was related* only to frequency measures of the former behaviours.

Rf - Op may be an intention operant response, in that it is a behaviour which closely resembles the first stage of many operant responses (those that involve no "detour" via the tank walls, for example). The positive relations* between this behaviour and search swimming may indicate that they share causal factors. It may be that the system which controls elevated swimming after loss of contact with a rival may also come to control the behaviour (operant responding) which achieves the reestablishment of contact.

The second group of post-reward behaviours are, with the exception of Op - Rf, those connected with a particular and distinctive pattern of behaviour. Instead of moving from the reward site to the operandum, the fish leaves in some other direction. This is usually followed by a period of wall swimming. After this, the fish may return to the reward site. The positive relations* between wall swimming and moves to and from the reward site may indicate that these have causal factors in common. Alternatively, they may be independently caused, but movements away from the reward site may lead the fish into the stimulus situation which elicits wall swimming. It may be that withdrawals which are not movements to the operandum are those which occur at low levels of motivation to perform the operant response. The problem with this interpretation is, however, that it is difficult to see why these withdrawals should be positively related* to wall swimming. The question of the nature of wall swimming is a difficult one. As has been pointed out, (ch. 8.2(a)) gill cover erection was never observed during

this behaviour, so it is unlikely to be an effect of reflections on the interior tank walls which elicits aggressiveness. The fact that this behaviour occurs in sexual contexts, albeit in a much more vigorous form, suggests that it may be a displacement activity of some kind. To speculate, if tendencies to perform the operant response and stay at the reward site do come into conflict, then wall swimming may be a result of heightened distractability during such conflict.

The behaviour Op - Rf was found to be negatively related* to a single search swimming behaviour (SeD(d)) and positively related to no other post-reward behaviour. This paucity of relations* means that there is little evidence to support a suggestion that this behaviour is causally linked to any other.

It has been suggested that post-reward behaviours inhibit operant responding. This hypothesis conflicts with the suggested causal relations between frequency measures of search swimming and the intention operant Rf - Op, but the way in which these behaviours have been quantified as rates means that the latter hypothesis cannot be tested with the present methods. This will be explained more fully in the following analysis which attempts to show that post-reward behaviours inhibit operant responding.

9.2 The Relations Between Post-Reward Behaviours and Operant Responding

9.2 (a) Introduction

The previous analysis showed that post-reward behaviours could be roughly divided into two groups, the first, consisting of behaviours associated with search swimming, and the second consisting of those related to wall swimming. In the first group, frequency measures of search swimming were positively

related* to Rf - Op, which is possibly an intention operant. From this it can be hypothesised that the frequency measures of search swimming and Rf - Op would be negatively related* to operant response latency, that is, caused by factors which also cause the operant response. This hypothesis cannot, however, be tested in the present analysis for the following reasons; when a post-reward behaviour is expressed as a rate measure (R) the amount of that behaviour (A) is divided by the operant latency during which it occurred (L). Thus, the rate of a post-reward behaviour is given by $R=^{A}/L$. To determine the relation* between the rate of post-reward behaviour (R) and the operant latency (L), R is correlated with L. The fact that $R=^{A}/L$ then poses problems of interpretation. If A varied little with increases in L, correlation of those two variables would result in a low nonsignificant correlation. However, since A is not correlated directly with L but instead is expressed in terms of L (giving R) and then correlated with L, a significant negative correlation between these variables may be found due solely to the use of a rate of measure. Thus, this analysis cannot distinguish between negative correlations due to this artifact, and those due to genuine relations between the behaviours of interest. For this reason, it will not be hypothesised that any post-reward behaviour will be negatively related to operant latency, and negative correlations when found will not be reported.

For the above reasons it will be hypothesised that the rates of all post-reward behaviours will be positively related* to operant latency.

9.2 (b) Method of Analysis

The three correlation methods (MCor, PCor and SCor) used in the previous analysis were applied here and the criterion for the demonstration of a relation* was used as before. Every post-reward behaviour has already been expressed as a rate measure, that is, divided by the operant latency in which it occurs and in this analysis was correlated

with that operant latency. Since predictions have been made about the signs of the correlations between post-reward behaviours and operant latency, significance testing was 1 - tailed.

9.2 (c) Results

When the criterion for demonstrating the existence of a relation* was applied in this analysis, only a single post-reward behaviour, Wls(d) was found to be positively related* to operant response latency (Op Lat) as hypothesised (Table 17). One possible reason for the failure to find consistent relations in the present analysis is that outlined previously. Where a behaviour varies little over subjects or sessions and where in a normal correlation procedure a low nonsignificant correlation would be found, the method of expressing one variable in terms of its rate of occurrence per unit duration of the second variable and then correlating it with that second variable can result in significant negative correlations. Given the ease with which negative correlations are found when rate measures are used the criterion for the demonstration of a significant relation* may be too stringent in this analysis and it was therefore temporarily suspended. Instead wherever a significant positive correlation was found, irrespective of the correlation method which produced it, that correlation will be tentatively accepted.

Table 17, shows the sizes and 1 - tailed significance levels of Spearman's rho between post-reward behaviours and operant latency. It can be seen that the behaviours SeS(d), SeD(d), Wls(f), Wls(d), Op - Rf, Ap and Wi were for at least one method positively correlated with operant latency. Since there remains the possibility that a serial order effect may produce significant correlations with methods MCor and PCor, most confidence can be placed in the result for Wls(d) (all methods positive, two significant); Ap and Wi (two methods significant and positive including method

SCor), SeS(d) and SeD(d) (method SCor significant). Less confidence can be placed in the relations between Op - Rf and Op Lat, (MCor and PCor positive, PCor significant) and Wlsf and Op Lat. (only PCor positive and also significant) since these may be due to a serial order effect. Fig. 28 shows schematically in decreasing order of certainty the relations between post-reward behaviours and operant latency.

9.2 (d) Discussion

Before accepting these results, an alternative explanation of the positive correlations found must be discounted. This alternative explanation concerns the expression of post-reward behaviours in terms of rates. It is possible that a positive correlation between the rate of a post-reward behaviour and operant latency could be found, not because that behaviour inhibits the operant response, but because the behaviour seldom occurs during short operant latencies. Such an occurrence is likely if post-reward behaviours are not evenly distributed during post reward intervals such that some behaviours tend to occur most often after a certain time into that latency. In the qualitive description of the behaviours occurring during operant sessions it was mentioned that the behaviour of swimming around the reward site, recorded in terms of its components SeS and SeD, tends to occur immediately after the reward terminates. It might be that other post reward behaviours, Op - Rf for example, occur only much later into the post reward interval and perhaps not at all when the operant latency is short. If this were the case, then a positive correlation between the rate of performance of Op - Rf and operant latency would be found. It might be erroneously concluded on the basis of such a correlation that Op - Rf inhibited operant responding when in fact it was equally probable that the operant latency was long for other reasons, and because the latency was long behaviours which only occur some time into post-reward intervals had the opportunity to occur.

To eliminate such a possibility it is not necessary to demonstrate that post-reward behaviours are equally distributed over the post reward interval. It is only necessary to show that the total amounts of these behaviours occurring during the actual operant latencies do not suddenly increase when the latency exceeds a certain duration. In other words a linear relationship must be shown to exist between operant latency and the absolute amounts of post reward behaviours, particularly over the short to middle range of latencies. The following analysis attempts to confirm this.

9.2 (e) The Relationship Between the Absolute Amounts of Post-Reward Behaviours and Operant Latency - Method of Analysis

For each of the 30 post reward intervals for each subject the means over subjects of the absolute amounts of post-reward behaviours were calculated. These mean amounts were then plotted against the mean duration of the intervals (the operant latencies) in which they occurred. These treatments were applied only to those behaviours which were shown in the previous analysis to be positively correlated with operant latencies, these being; Wls(f), Wls(d), AP, Wi, SeS(d), SeD(d) and Op - Rf.

9.2 (f) Results

Figs. 29 - 35 show scattergrams depicting relations between the means of the absolute amounts of Wls(f), Wls (d), SeS(d), SeD(d), AP, Wi and Op - Rf, and mean operant latencies. In no case is there any indication that short operant latencies show disproportionately low levels of these post-reward behaviours.

9.2 (g) Discussion

No evidence was found that the relations between the absolute amounts of post reward behaviours and the operant response latencies in which they occurred, were other than

linear. Thus, the correlations between the rates of occurrence of post-reward behaviours and operant latency cannot be explained as an artifact of their expression as rates. It must be concluded, then, that some post-reward behaviours actually inhibit operant responding. This is most certain for Wls(d) since it satisfied the criterion for a relation*.

It is interesting to note that the frequency measures of search swimming and the intention operant Rf - Op, were not positively correlated with operant latency when any of the three correlation methods were used. Although the present methods of analysis cannot produce evidence that these behaviours share causation with operant responding, no evidence contrary to this hypothesis has emerged.

Some post-reward behaviours of both of the groups identified earlier are inhibitory towards operant responding. The relations* between post reward behaviours do not, therefore, reflect their relations with operant latency.

A question which must be asked about operant response-inhibiting post-reward behaviours concerns the sources of variation in these behaviours. That is, do other processes or tendencies influence the tendency to perform post reward behaviours. It has earlier been shown that some reward elicited behaviours were negatively related* to operant latency. It can be suggested that the action of these behaviours of operant latency is not direct, but mediated by their effects of post-reward behaviours. Thus, although it may be the case that the attack tendency directly motivates operant responding, it is also possible that attack decreases operant latencies by inhibiting post-reward behaviours. By similar reasoning, lateral display duration may represent the state of a system which inhibits operant responding. A more parsimonious interpretation of the relations* between LD(d) and operant latency, however, may be that it facilitates operant response-inhibiting post-reward behaviours.

It has been suggested that since the two measures of search swimming - SeS(f) and SeD(f) - were positively related* to the intention operant Rf - Op, they may be related to the tendency to perform operant responses. This hypothesis could not be tested for the reasons outlined in ch. 9.2(a) but an indirect test is possible. If SeS(f), SeD(f) and Rf - Op do share causal factors with operant responding, then they should be positively related* to those reward-elicited behaviours (Bi, Bu(f), Bu(d) and AG(f) which are negatively related* to operant response latency. It also follows that they should be negatively related* to the reward-elicited behaviour LD(d) which is positively related* to operant latency.

The following analysis investigates the relations between reward-elicited and post-reward behaviours.

9.3 The Relations Between Reward Elicited and Post Reward Behaviours

9.3 (a) Introduction

It was suggested that the relations* between reward-elicited behaviours and operant latency found in ch. 8.4 could be accounted for, in part at least, by their effects on post-reward behaviours. The following relations* were predicted.

1. Those reward-elicted behaviours negatively related* to operant latency (Bi, Bu(f), Bu(d) and AG(f) will be negatively related* to the rates of those post-reward behaviours positively correlated with operant latency (SeS(d), SeD(d), Wls(d), Wls(f), Op - Rf, AP and Wi).
2. The reward-elicited behaviour positively related* to operant latency (LD(d)) will be positively related* to those post-reward behaviours positively correlated with operant latency (SeS(d), SeD(d), Wls(f), Wls(d), Op - Rf, AP and Wi).

3. The post reward behaviours SeS(f) and the intention operant Rf - Op, will be positively related* to Bi, Bu(f), Bu(d) and AG(f), and negatively related* to LD(d).

9.3 (b) Method of Analysis

The data used in this analysis concerned the same rewards and operant latencies as the preceding analysis. The amounts of all reward-elicited behaviours were correlated (Spearman's rho) with rate measures of all post-reward behaviours. The criterion for the finding of a relation* was applied as before. Since some directional predictions have been made, significance testing of the correlations obtained will be 1 - tailed. For all reward-elicited and post-reward behaviours about which directional predictions have not been made, significance testing will be 2 - tailed.

9.3 (c) Results

Table 18 shows the sizes and significance levels (1-tailed) of the correlations between those reward-elicited behaviours shown earlier to be related* to operant response latency, and the post-reward behaviours (SeS(f), SeD(f)) positively related* to the intention operant Rf - Op. Fig. 36 shows schematically the relations* found. It can be seen that those reward-elicited behaviours which were negatively related* to operant response latency are here often positively related* and never negatively related* to SeS(f), SeD(f) and the intention operant Rf - Op. The reward elicited behaviour LD(d) which was shown to be positively related* to operant latency was never positively related* to the three post-reward behaviours being considered here, and was negatively related* to two of them (SeS(f) and Rf-Op). These relations* provide evidence to support the suggestion that these three post-reward behaviours are caused by factors which also cause the operant response.

Table 19 shows the sizes and significance levels (2 - tailed) of correlations between reward-elicited behaviours not previously implicated in the control of operant responding and all post-reward behaviours. Fig. 37 shows that where relations* were found, they were always positive, and two reward-elicited behaviours (LD(d) and FD(f)) were each related* to only a single post reward behaviour (Rf-Op and Wi respectively).

Table 20 shows the sizes and significance levels (1 - tailed) of the correlations between reward-elicited behaviours earlier implicated in the control of operant responding and post-reward behaviours shown to be inhibitory towards operant responding. It can be immediately seen that several of the correlations found were not in the predicted direction. Where this has occurred, the significance levels of these correlations are not given. For only one post-reward behaviour (Op-Rf) are correlations not in the predicted direction significant over the three correlation methods used. To avoid loss of information, the correlations for Op-Rf were tested for 2 - tailed significance (Table 21). Only the positive relation* between Op-Rf and Bi was significant with this procedure.

Fig. 38 shows schematically the relations* between reward-elicited behaviours implicated in the control of operant responding, and the post-reward behaviours which inhibit responding. From this, it can be seen that only three post-reward behaviours are related* to operant-controlling reward-elicited behaviours, namely Wls(d), Wi and Op-Rf. As predicted, reward-elicited behaviours negatively related* to operant response latency were positively related* to the response-inhibiting post-reward behaviours Wls(d) and Wi. The behaviour LD(d), positively related* to operant latency, was positively related* to Wls(d). It is interesting to note that Wls(d) is the post-reward behaviour whose inhibitory relation to operant responding was most certain since it satisfied the criterion for a relation*.

Contradicting the hypothesis that operant response-inhibiting post-reward behaviours would be negatively related* to reward-elicited behaviours themselves negatively related* to operant response latency, is the positive relation* found between biting and Op-Rf. Thus, Bi inhibits some response-inhibiting post reward behaviours but facilitiates another.

9.3 (d) Discussion

Evidence was found to support the hypothesis that some post-reward behaviours (SeS(f), SeD(f) and Rf-Op) are controlled by causal factors which also motivate operant responding. The evidence presented concerned the relations* between these post-reward behaviours and reward-elicited behaviours. These relations* corresponded to those found between the reward-elicited behaviours and operant latency.

The relations* between reward-elicited behaviours which were not earlier found to be related to operant latency and post-reward behaviours, were positive. Thus, post-reward behaviours which inhibit the operant response can be facilitated by reward-elicited behaviours which are not themselves positively related* to operant latency.

If only those reward-elicited and post-reward behaviours are considered which have been implicated in the control of operant responding, the results of the previous analysis to a considerable extent confirm the hypothesis advanced. That is, the relations* between reward-elicited behaviours and operant latency can be accounted for by their relations* with response-inhibiting post-reward behaviours. The only exception to this is AG(f), which, although negatively related* to operant response latency, was not found to be related* to any response-inhibiting post-reward behaviour.

The relations* between biting and response-inhibiting post-reward behaviours were found to be complex, in that it

was negatively related* to two such behaviours (withdrawal and wall swimming duration) and positively related* to another (swimming from the operandum to the reward site).

The relations between reward elicited behaviours other that AG(f), and operant latency, may be mediated to some extent by their effects on post-reward behaviours. There remains, however, the possibility that a direct effect coexists with these, such that the motivational states aroused by reward determine the strength of the motivation to perform operant response. However, an alternative interpretation of the relations* between reward elicited behaviours and operant latency may be advanced. The possibility must be considered that the operant response latency determines the levels of the various behaviours that rewards elicit. It was remarked in Ch. 8.2 (g) that fewer bites were elicited by 15mins. of intermittent conspecific stimulation (rewards) than were elicited by 15mins. of continuous stimulation in an earlier experiment (Experiment 1). It was suggested that the interval between rewards may act to lower the attack tendency. In addition, the demonstration in ch. 8.2 that during operant sessions the frequency of biting to rewards increases, implied that exposure to a displaying rival conspecific increases the attack tendency. The occurrence of facilitation in attack implies that when stimulation ceases, i.e. between periods of stimulation, the attack tendency decays. If attack was controlled by such a process, then it would be expected that in an operant situation, short operant latencies (inter-presentation intervals) would produce higher levels of biting. The same may apply to the other reward-elicited behaviours related* to operant latency, in that the amounts of these produced by reward may be determined by the operant latencies which occur.

The following chapter reports an investigation of the effects of stimulus inter-presentation interval on some aggressive behaviours.

Figure 27

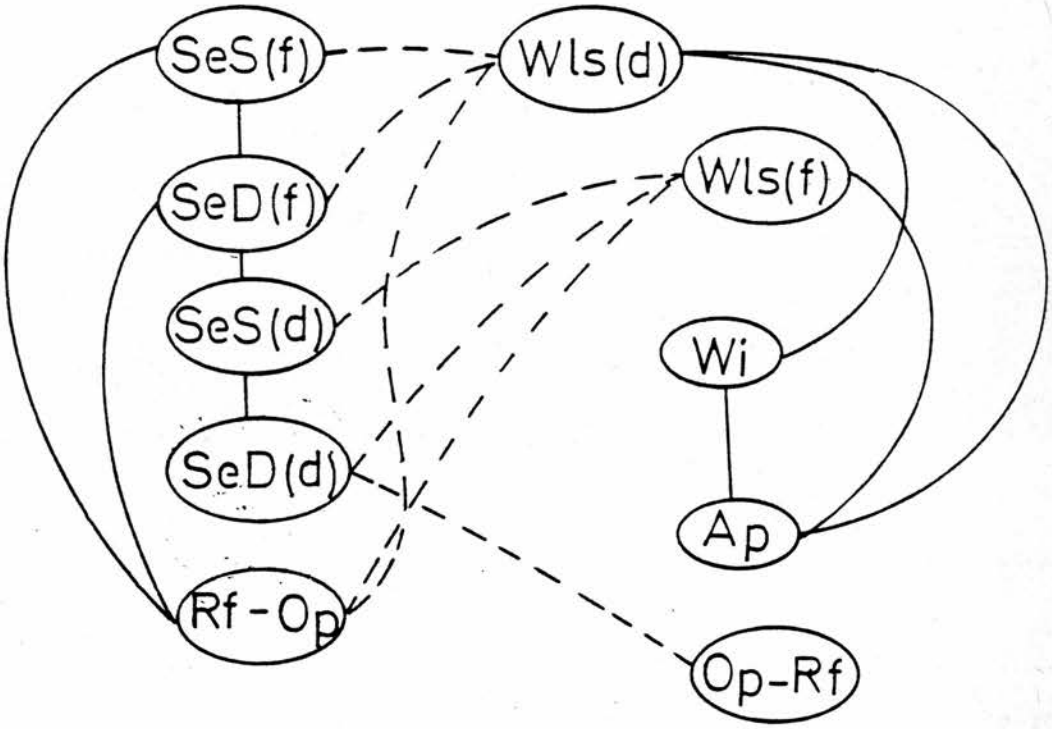
The relations* between post-reward behaviours.

Positive relations* indicated by ——————

Negative relations* indicated by — — — —

Figure 28

The positive correlations between between post-reward behaviours and operant latency (Op. Lat.) in decreasing order of certainty.


SeS(f)
Wls(d)
SeD(f)
Wls(f)
SeS(d)
Wi
SeD(d)
Ap
Rf - Op
Op-Rf

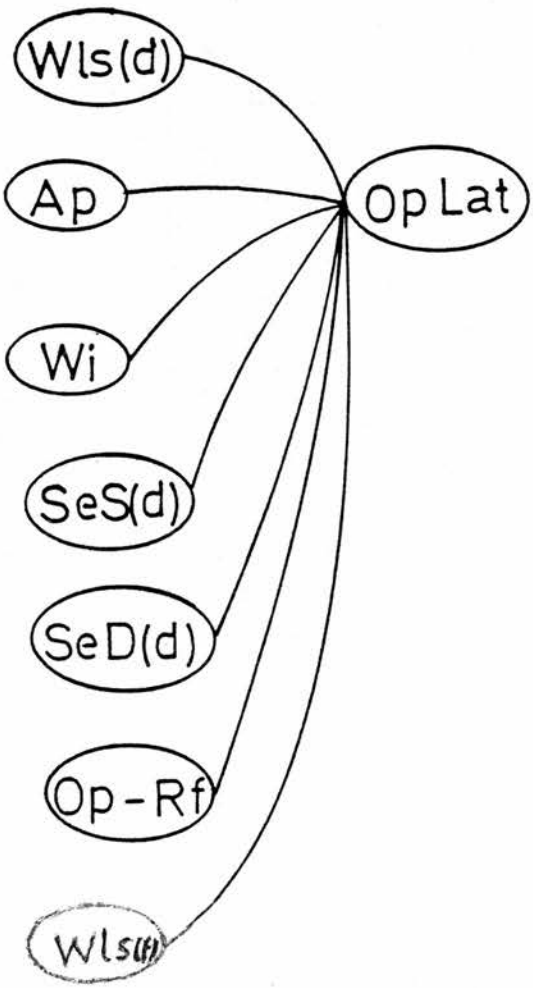

Wls(d)
Ap
Op Lat
Wi
SeS(d)
SeD(d)
Op-Rf
Wls(f)

Figure 29

Mean Wall swim frequency (Wls(f)) as a function of mean operant latency (Op. Lat.). N = 30.

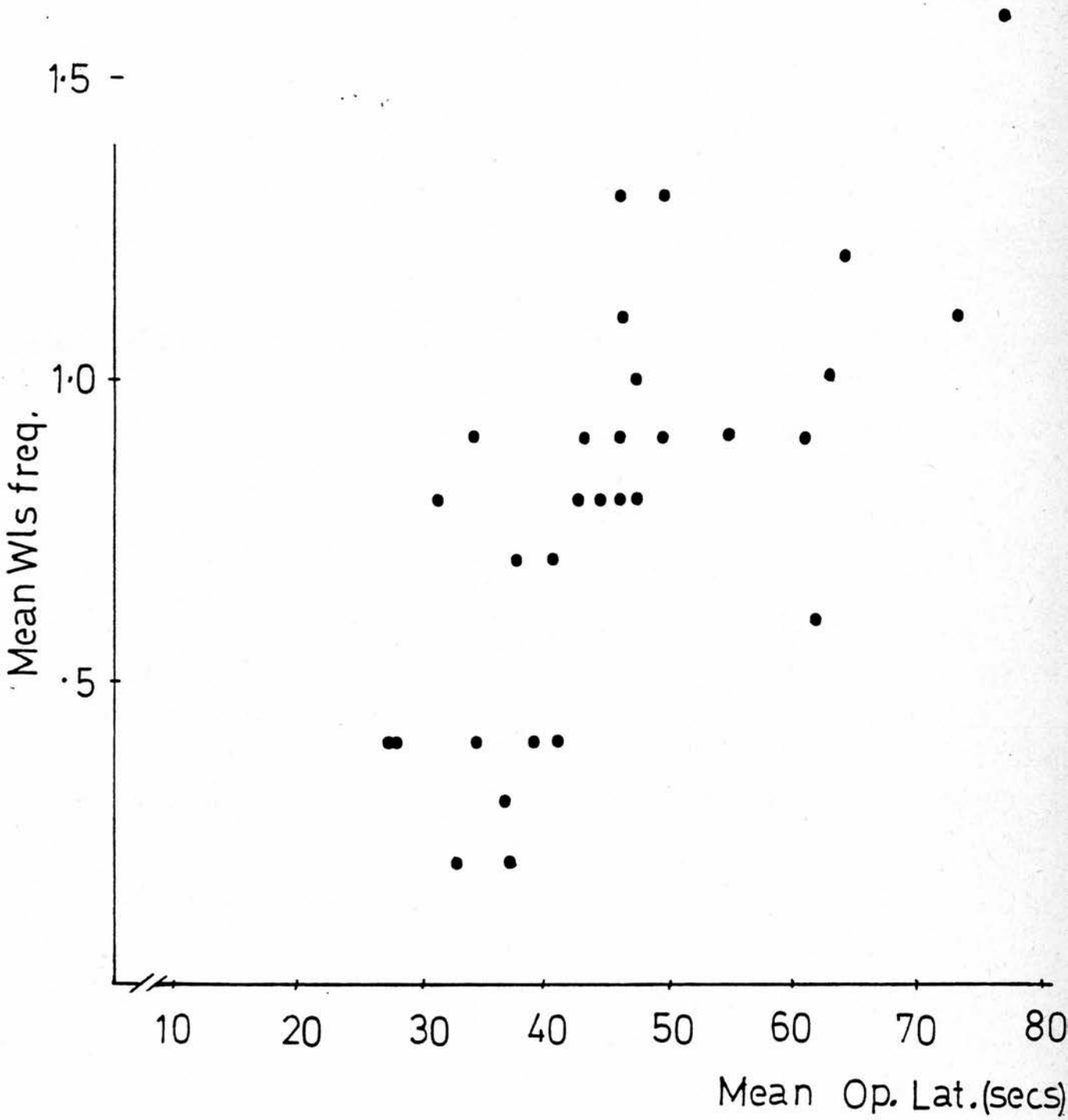

1·5
1·0
·5
Mean Wls freq.
10
20
30
40
50
60
70
80
Mean Op. Lat.(secs)

Figure 30

Mean wall swim duration (Wls(d)) as a function of mean operant latency (Op. Lat.). N = 30.

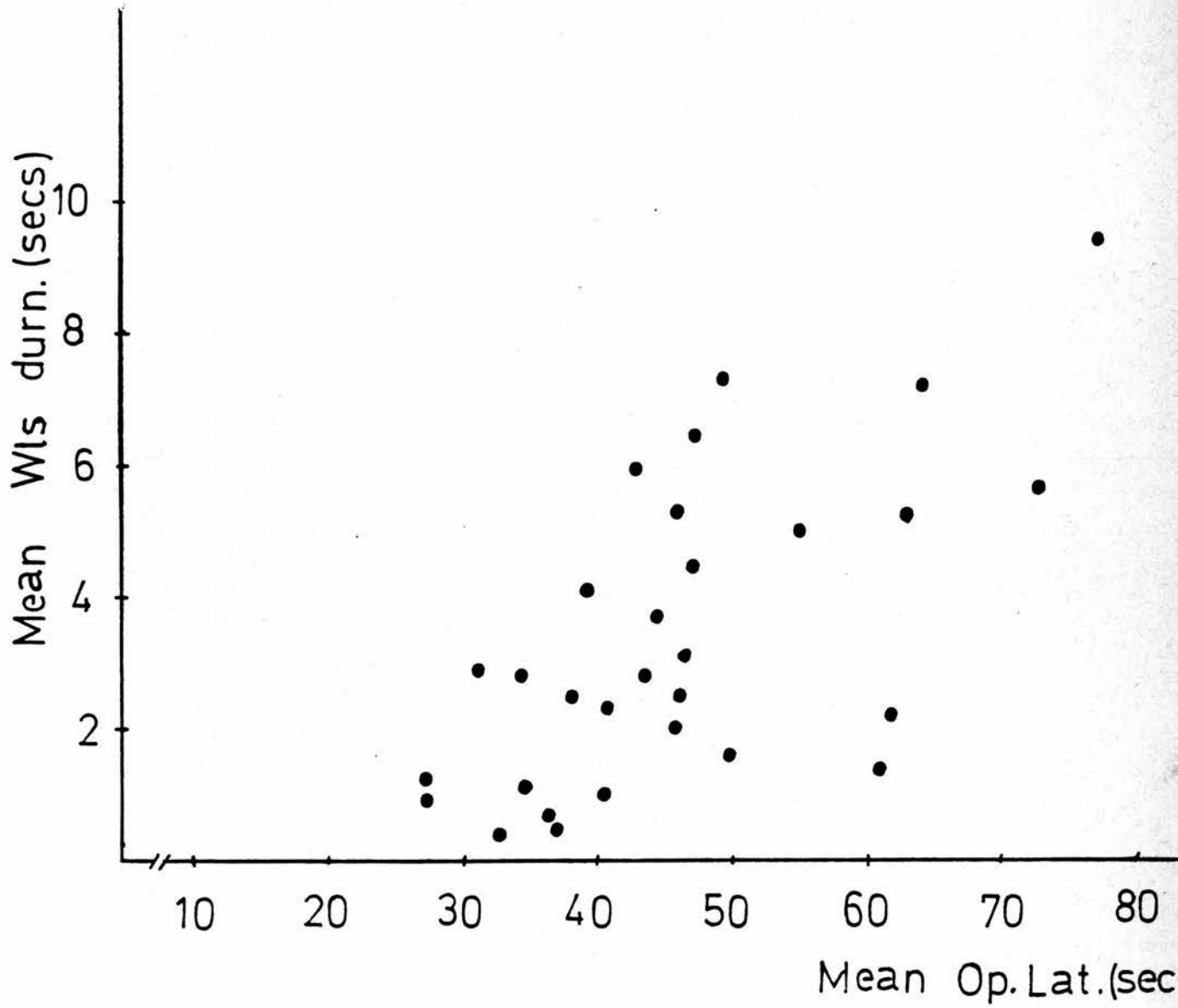

Mean Wls durn. (secs)
10
8
6
4
2
10
20
30
40
50
60
70
80
Mean Op. Lat. (sec

Figure 31

Mean search swim (SeS) duration as a function of mean operant latency (Op. Lat.). N = 30.

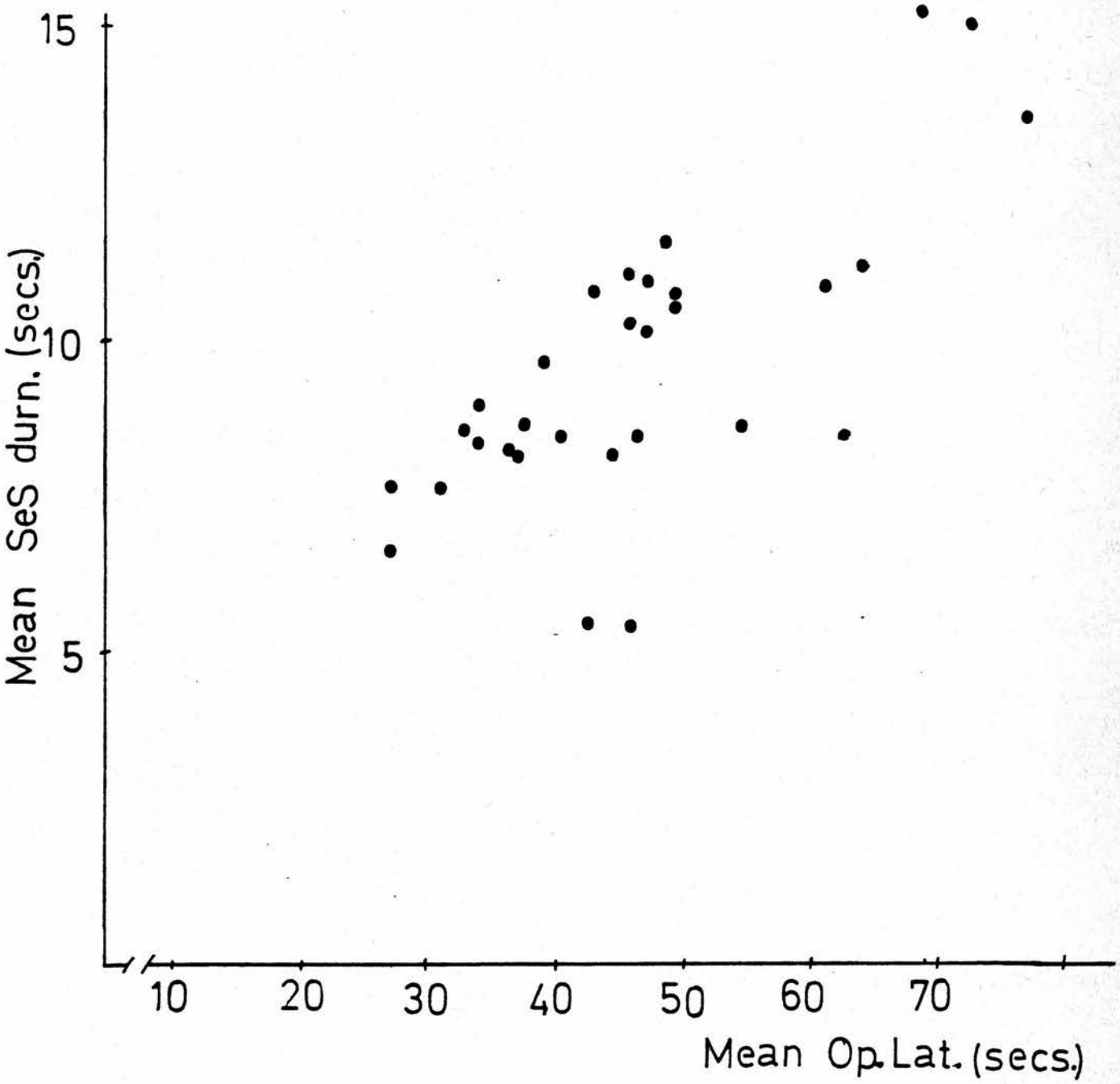

15
10
5
Mean SeS durn. (secs.)
10
20
30
40
50
60
70
Mean Op. Lat. (secs.)

Figure 32

Mean search swim with dorsal erect (SeD) duration as a function of mean operant latency (Op. Lat.). N = 30.

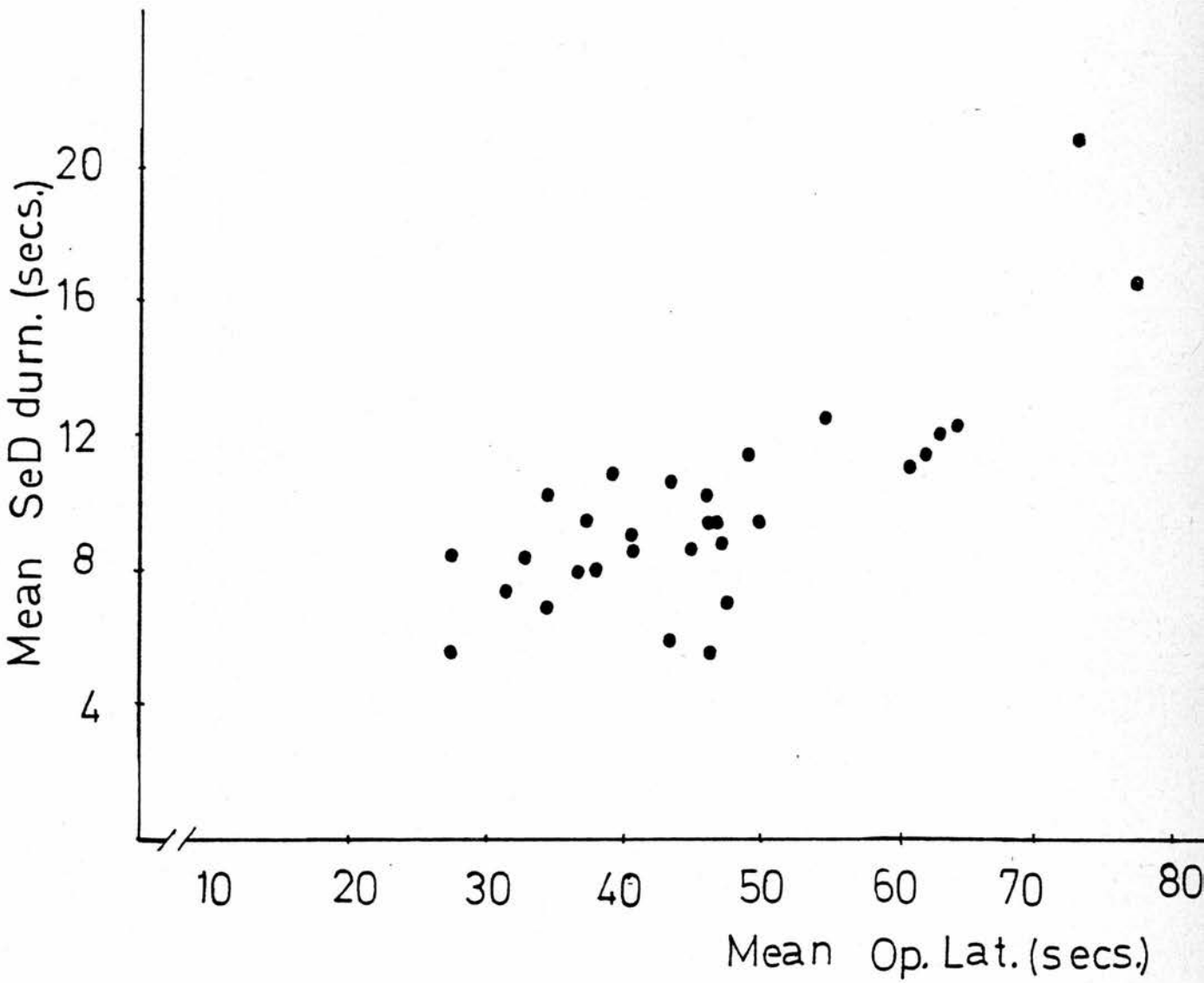

Mean SeD durn. (secs.)
20
16
12
8
4
10
20
30
40
50
60
70
80
Mean Op. Lat. (secs.)

Figure 33

Mean approach frequency (Ap) as a function of mean operant latency (Op. Lat.). N = 30.

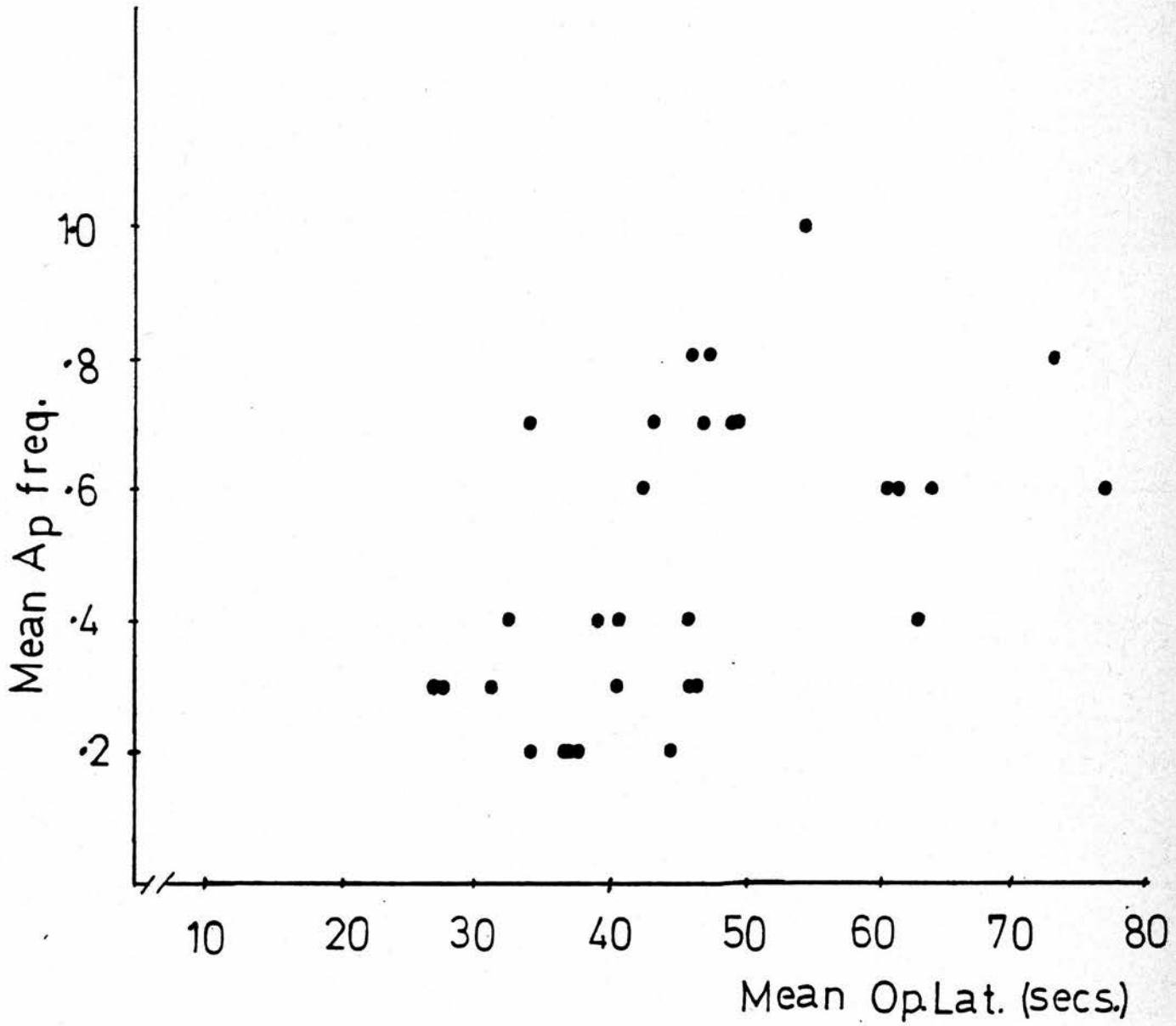

Mean Ap freq.
1·0
·8
·6
·4
·2
10
20
30
40
50
60
70
80
Mean Op.Lat. (secs.)

Figure 34

Mean withdrawal (Wi) frequency as a function of mean operant latency (Op. Lat.). N = 30.

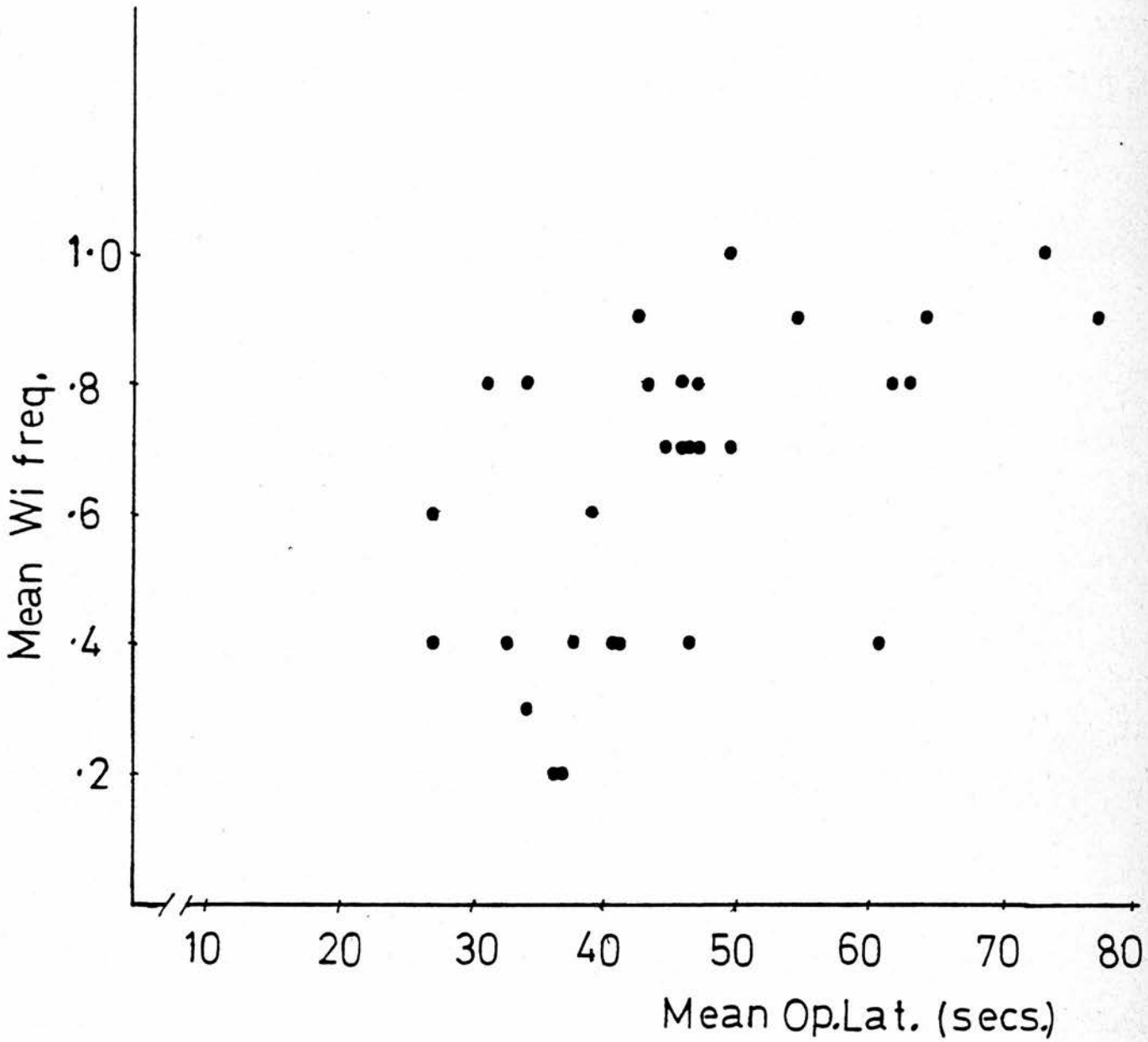

1·0
·8
·6
·4
·2
Mean Wi freq.
10
20
30
40
50
60
70
80
Mean Op.Lat. (secs.)

Figure 35

Mean movements from the operandum to the reinforcement site (Op - Rf) as a function of mean operant response latency (Op.Lat.).

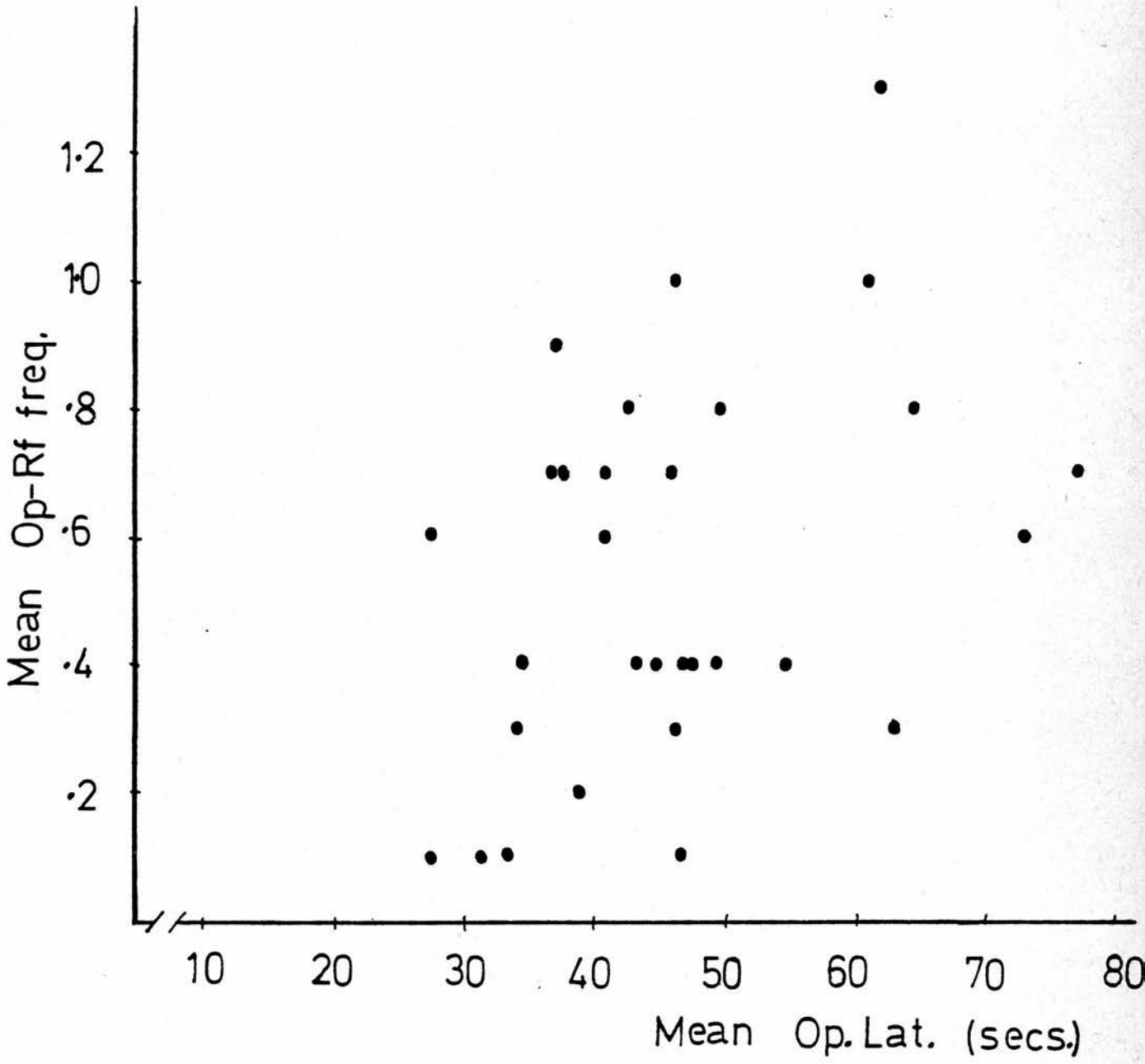

1·2
1·0
·8
·6
·4
·2
Mean Op-Rf freq.
10
20
30
40
50
60
70
80
Mean Op. Lat. (secs.)

Figure 36

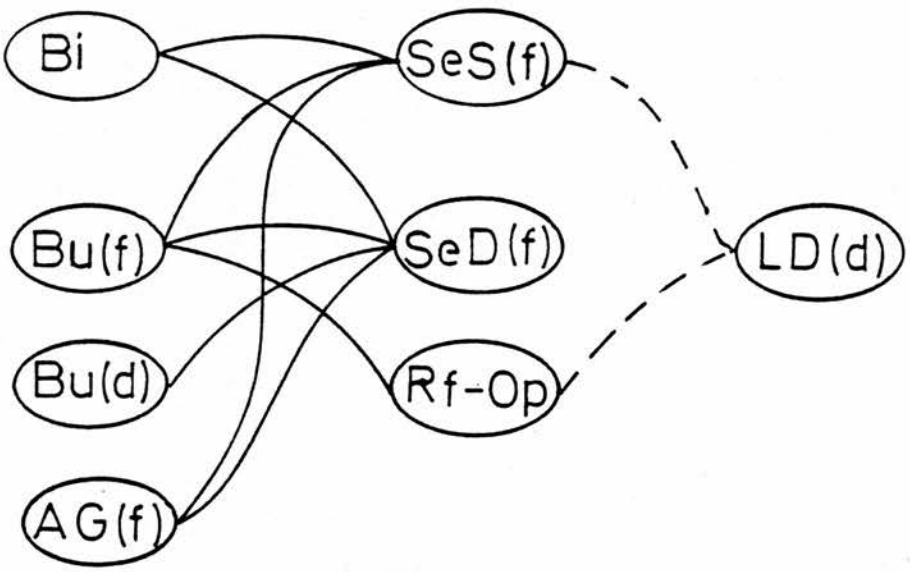
The relations* between reward-elicited behaviours and those post-reward behaviours hypothesised to be causally related to operant responding.

Positive relations* represented by ———

Negative relations* represented by – – – –

Figure 37

The relations* between reward-elicited behaviours not related to operant latency and post-reward behaviours.


Bi
Bu(f)
Bu(d)
AG(f)
SeS(f)
SeD(f)
Rf-Op
LD(d)

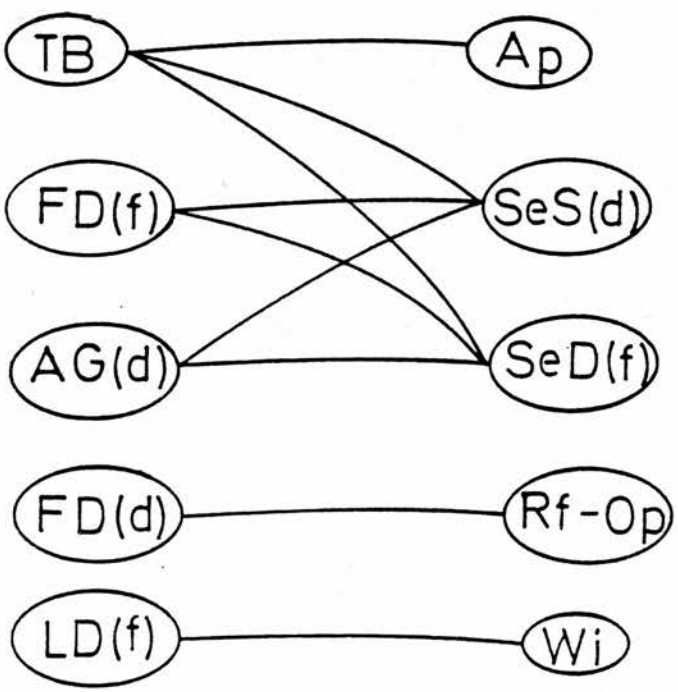

TB
FD(f)
AG(d)
FD(d)
LD(f)
Ap
SeS(d)
SeD(f)
Rf-Op
Wi

Figure 38

The relations* between reward-elicited and post-reward behaviours related to operant latency.

Positive relations* indicated by _____

Negative relations* indicated by _ _ _ _

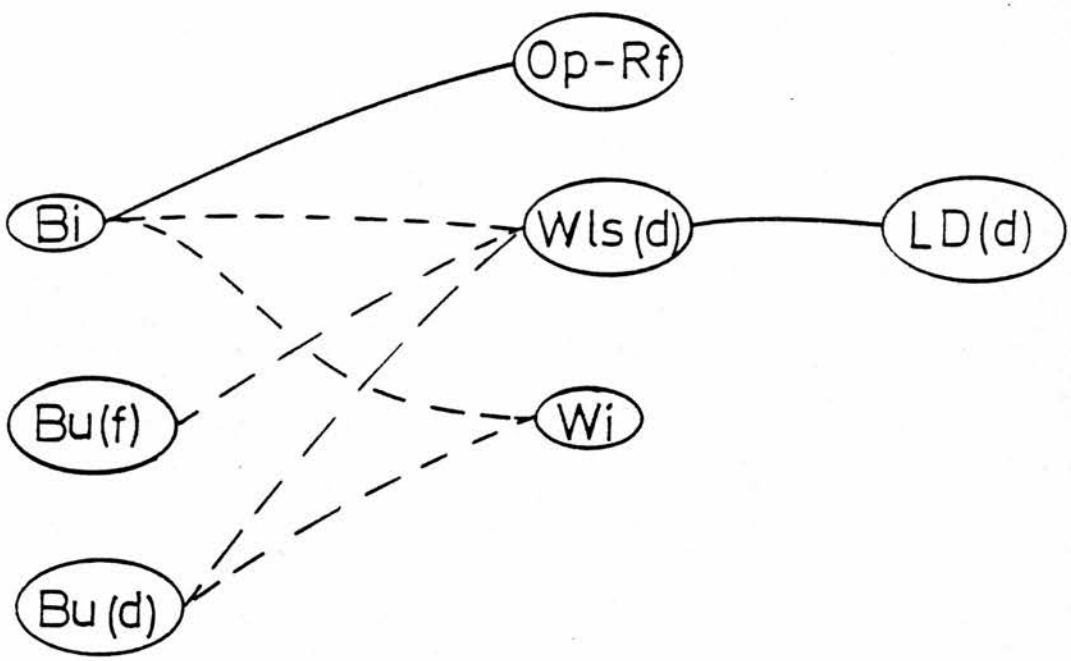

Op-Rf
Bi
Wls (d)
LD (d)
Bu (f)
Wi
Bu (d)

Table 16

The Spearman correlations between the rates of post-reward behaviours. Significance levels given are 2-tailed.

	SeS(d)	SeD(f)	SeD(d)	Wls(f)	Wls(d)	Rf-Op	Op-Rf	Ap	Wi	
	.708	.916	.514	-.044	-.397	.264	-.243	.053	-.138	M
SeS(f)	.652	.915	.384	-.267	-.341	.400	-.085	-.113	-.108	P
	-.700	.333	-.800	.773	-.750	.300	.600	-.150	-.550	S
		.756	.704	-.263	-.411	.222	-.187	.030	-.267	M
SeS(d)		.619	.376	-.354	-.357	.187	-.091	-.166	-.179	P
		.067	.850	-.656	.583	-.133	-.483	.350	.733	S
			.584	-.110	-.321	.161	-.186	.074	-.119	M
SeD(f)			.431	-.303	-.370	.386	-.077	-.124	-.141	P
			-.033	.387	-.183	.100	.567	.417	.083	S
				-.294	-.488	.147	-.196	-.073	-.280	M
SeD(d)				-.431	-.452	.161	-.133	-.288	-.329	P
				-.782	.533	-.033	-.533	.200	.533	S
					.678	-.500	-.126	.243	.752	M
Wls(f)					.935	-.432	.015	.528	.764	P
					-.756	-.277	.882	.286	-.723	S
						-.665	-.128	.105	.694	M
Wls(d)						-.518	-.001	.498	.721	P
						-.117	-.567	.067	.817	S
							.393	.108	-.592	M
Rf-Op							.319	-.139	-.491	P
							-.383	-.783	.200	S
								-.010	-.212	M
Op-Rf								.022	-.040	P
								.533	-.617	S
									.442	M
Ap									.629	P
									.017	S

			Indicated by
MCor (M)	N = 30	$p < .02$	———
PCor (P)	N = 270	$p < .05$	- - - - -
SCor (S)	N = 9	$p < .02$	———

Table 17

The Spearman correlations between the rates of post-reward behaviours and operant latency. Only positive correlations are given and significance levels are 1-tailed.

	SeS(f)	SeS(d)	SeD(f)	SeD(d)	Wls(f)	
Op.Lat.						MCor
					.220	PCor
		.750		.800		SCor

	Wls(d)	Rf-Op	Op-Rf	Ap	Wi	
Op.Lat.	.262		.163			MCor
	.344		.320	.333	.185	PCor
	.750			.317	.533	SCor

1-tailed	represented by
$p < .05$	- - - - -
$p < .01$	———

Table 18

The Spearman correlations between operant controlling reward-elicited behaviours and post-reward behaviours hypothesised to be causally related to operant responding.

	SeS(f)	SeD(f)	Rf-Op	Method	
	.286	.255	.598	MCor	
Bi	.118	.102	.281	PCor	
	.653	.686	-.034	SCor	
	.342	.328	.473	Mcor	
Bu(f)	.072	.061	.276	PCor	
	.695	.661	.209	SCor	
	.299	.312	.487	MCor	
Bu(d)	.068	.057	.274	PCor	Positive correlations
	.285	.745	-.142	SCor	predicted.
	.299	.148	.402	MCor	
AG(f)	.179	.173	.136	PCor	
	.326	.276	-.059	SCor	
	-.335	-.321	-.414	MCor	
LD(d)	-.029	.044	-.164	PCor	Negative correlations
	-.433	-.317	-.083	SCor	predicted.

1-tailed significance levels		Method	N
$p < .05$	represented by _ _ _ _ _	MCor	30
$p < .01$	" " ———	PCor	270
		SCor	9

Table 19

The Spearman correlations between reward-elicited behaviours not related* to operant latency and all post-reward behaviours.

	SeS(f)	SeS(d)	SeD(f)	SeD(d)	Wls(f)	Wls(d)
	.372	.013	.325	.037	-.160	-.407
TB	.295	.217	.293	-.087	.136	.081
	-.544	.870	.193	.720	-.418	.310
	.294	.049	.202	.126	.244	-.235
FD(f)	.189	.128	.206	.098	.053	.025
	-.367	.550	.133	.200	-.210	.483
	.149	-.016	.070	.044	.038	-.174
FD(d)	.118	.005	.086	-.068	.024	-.045
	-.333	.250	-.250	-.050	-.294	.433
	.246	.074	.139	.156	.311	-.191
LD(f)	.113	.083	.157	.102	.081	.053
	-.200	.683	-.017	.483	-.319	.297
	.374	.183	.411	.040	-.118	-.206
AG(d)	.174	.132	.164	-.051	.079	.078
	-.533	.633	.017	.433	-.546	.450

	Rf-Op	Op-Rf	Ap	Wi
	.490	.383	.073	-.239
TB	.134	-.069	.145	.180
	-.201	-.251	.527	.572
	.273	.106	.058	-.031
FD(f)	.097	.006	.068	.105
	-.267	-.300	.350	.683
	.396	.296	.121	-.076
FD(d)	.120	.129	.000	.019
	-.033	-.500	-.183	.600
	.050	.097	-.063	.075
LD(f)	.048	.030	.089	.121
	-.150	-.317	.317	.400
	.302	.059	.197	-.049
AG(d)	.114	-.037	.058	.075
	.217	-.600	-.100	.767

Method	2-tailed significance levels
MCor	$p < .02$ represented by _____
PCor	$p < .05$ " " - - - -
SCor	$p < .02$ " " _____

Table 20

The Spearman correlations between reward-elicited behaviours and post-reward behaviours implicated in the control of operand responding. Where correlations are not in the direction predicted, no significance level is given.

	SeS(d)	SeD(d)	Wls(f)	Wls(d)	Op-Rf	Ap	Wi	Method	
	.071	.201	-.281	-.515	.377	-.114	-.412	MCor	-
Bi	-.015	.066	-.107	-.154	.103	-.092	-.125	PCor	-
	-.444	-.444	.831	-.795	.829	.293	-.603	SCor	-
	.128	.281	-.301	-.476	.276	.050	-.291	MCor	-
Bu(f)	-.038	.022	-.081	-.101	.083	-.021	-.081	PCor	-
	-.611	-.536	.696	-.628	.745	.092	-.460	SCor	-
	.070	.162	-.391	-.487	.247	-.033	-.333	MCor	-
Bu(d)	-.042	.012	-.080	-.098	.082	-.015	-.079	PCor	-
	-.268	-.142	.519	-.368	.678	.477	-.285	SCor	-
	.054	-.175	-.053	-.218	.041	.090	-.032	MCor	-
AG(f)	.133	-.030	.081	.050	.018	.044	.072	PCor	-
	-.352	-.075	.249	-.151	.511	.201	-.418	SCor	-
	-.190	.090	.111	-.189	-.015	-.161	.171	MCor	+
LD(d)	.062	.058	.084	.096	.024	.131	.099	PCor	+
	.450	.150	-.387	.433	-.517	.017	.633	SCor	+

1-tailed significance levels	Method	N
$p < .05$ represented by _ _ _ _	MCor	30
$p < .01$ " " ———	PCor	270
	SCor	9

\- = negative correlations predicted

\+ = positive correlations predicted

Table 21

The Spearman correlations between Op-Rf and reward-elicited behaviours related* to operant latency.

	Bi	Bu(f)	Bu(d)	AG(f)	LD(d)	Method
	.377	.276	.247	.041	-.015	MCor
Op-Rf	.103	.083	.082	.018	.024	PCor
	.829	.745	.678	.511	-.517	SCor

Method	N	2-tailed significance levels
MCor	30	$p < .02$ represented by _____
PCor	270	$p < .05$ represented by _ _ _ _
SCor	9	$p < .02$ represented by _____

CHAPTER 10

10.1 The Effect of Stimulus Interpresentation Interval on Aggressive Behaviour - Experiment 7

10.1 (a) Introduction

The relations between all reward elicited behaviours and operant latency could be explained by the hypothesis that all behaviours are determined by the inter-reward interval. To test this hypothesis, stimulus presentations can be made at various intervals, without any operant requirement, and their effect on attack and display observed. The following experiment seeks to discover whether those reward-elicited behaviours earlier implicated in the control of operant responding, Bi, Bu(f), Bu(d), AG(f) and LD(d), are independent of the stimulus inter-presentation interval.

10.1 (b) Subjects and Stimulus Fish

Ten male Betta splendens were randomly selected from those kept under initial maintenance conditions which had nest volumes of less than .4cms.^{3} Some of the subjects selected had been used in previous experiments.

From the remaining stock of males, 10 Bettas were randomly chosen to act as stimulus males. These fish included males with and without nests and they were allocated to individual subjects by the method used in the previous experiment. Stimulus males subordinate to a subject were rejected for that subject and tested with others after an interval exceeding 30mins.

In this experiment, the stimulus selection test was also used to evaluate the suitability of subjects. During the test, the behaviour of subjects was observed. If any withdrawals from the stimulus were shown between minutes 3 and 5 of the test, then that subject was discarded and replaced. This occurred for 3 subjects while no stimulus

fish failed to display to at least one subject. The criterion for withdrawal was the same as that used for Experiment 1. Rejected subjects were replaced by males randomly selected from stock and having nest volumes not exceeding .4cms^3. In addition to subjects and stimulus fish, 2 stimulus pre-treatment males were selected by the same method as that used in the previous experiment. The selection of fish to be used, their transference to experimental maintenance conditions and subsequent testing was carried out in two batches, each of 5 subjects and stimulus fish. The testing of the two batches was separated by 7 days and the same stimulus pretreatment males were used for both batches.

10.1 (c) Apparatus

The apparatus used in the previous operant experiment presented the stimulus fish in its container for approximately 30secs., contingent on the operant response of the subject. For the present experiment, the subject's control over the stimulus was removed, and instead, presentations occurred automatically at preset intervals. This was achieved by inserting a pulse generating timer into the presentation control circuit in place of the output from the operant response gate. The throwing of a switch mounted on the table in front of the experimenter simultaneously illuminated the chamber light and initiated the series of presentations. After 30 presentations the series was terminated.

10.1 (d) Presentations and Inter-Presentation Intervals

The duration of the stimulus presentation was the same as used in the previous operant experiment, varying from 30secs. to approximately 34secs. depending on the behaviour of the subject and stimulus fish. For the same reason the inter-presentation interval (IPI) as determined by the timer may not be the actual interval between periods of visual

contact. An IPI of 1sec. is the interval between the termination of one presentation, that is, when the stimulus cover has descended to the level of the substrate, and the initiation of the following presentation. However, on the termination of a presentation, visual contact between the subject and stimulus may cease some time before the cover reaches the substrate, and not be reestablished until the cover has been raised some distance again. An IPI nominally of one second may therefore have an actual value of between 1sec. and 5secs. After the experiment the actual value of each IPI was determined empirically by measuring the time during which fish appear to the experimenter not to be in visual contact. These were as follows for IPI's 1, 10, 30 and 70 respectively: 1.8, SEM = .1; 12.0, SEM = .6; 32.7, SEM = .9; 72.5, SEM = 1.0secs.

Since the intention here was to compare the amounts of behaviours occurring during presentations of similar duration but separated by differing inter-presentation intervals, and since one of these intervals was 0secs., the data from the IPI(0) condition must be made comparable with those from IPI's of greater duration. IPI(0) sessions which are continuous must therefore be broken down into 30 segments, each segment of which is of a duration comparable to those of presentations at other IPI's. Since presentation durations differ due to the behaviour of the fish concerned, it is not possible to decide in advance the precise appropriate duration of the long presentation which is IPI(0). That is, if presentations were uniformly 30 seconds long, then the appropriate duration of the continuous IPI(0) session would be 15mins. (30 x 30 secs.), but since presentations differ in duration, all that was known before the experiment was that presentations can have a maximum duration of 34secs., and a total maximum stimulus exposure duration of 18.3mins. For this reason, IPI(0) sessions were of longer duration than this maximum (19mins.). The actual duration of presentations at other IPI's was then determined empirically and the IPI(0) session was adjusted in duration before data analysis. Taking

an example, if a particular subject had a mean presentation duration of x secs. over IPI's of 1, 10, 30 and 70secs., then only the first 30xsecs. of its IPI(0) session was used in data analysis and the remaining 19mins. - 30x secs. was discarded. This was performed for each subject individually. By this means it was possible to compare not only whole sessions at different IPI's, but also behaviour at any particular presentation during the session. This was achieved by breaking the IPI(0) session into successive intervals of a size equal to the empirically determined mean presentation duration at other IPI's.

10.1 (e) Experimental Design

Each of the 10 subjects was tested 6 times, once daily. A test consisted of 30 stimulus presentations of approximately 30 secs. each, separated by an inter-presentation interval nominally of one of the following durations: 0, 1, 10, 30 and 70 secs. (the actual durations are given in 10.1 (d)). The first day of testing of each subject was with an IPI of 10 secs. to allow some degree of habituation to the test situation to occur. In addition, a pilot experiment revealed that the rate of biting in subjects increases markedly from the first day of testing to the second and thereafter increases much more slowly, if at all. The first test during which behaviour was recorded but from which data was not used in analysis, removed much of the variance due to this relatively long-term change in attack tendency.

After the first day of testing at IPI(10) each subject was tested with IPI's of 0, 1, 10, 30 and 70 secs. over 5 days. The order in which the various IPI's were used was determined by a randomised block design. Subjects were divided randomly into two groups of 5, each subject being tested in 5 conditions (IPI's). The order of conditions was determined by two independently generated 5x5 tables, such that over each group

of 5 subjects a particular condition was represented once in every serial position (see Fisher, 1951, p. 72; Fisher and Yates, 1935).

10.1 (f) Procedure

The preliminary procedures, including subject and stimulus pre-treatment were identical to those used in the preceding experiment. No biting occurred during these pre-treatment procedures. The IPI condition for a particular subject and test was determined from the test schedule (5x5 table) which included that subject, and the stimulus presentation apparatus set at that value. In the previous operant experiment an interval of 60secs. was allowed after subject pre-treatment before the chamber light was illuminated, and therafter the first presentation was contingent on the subject's behaviour. In this experiment, subject pre-treatment was followed by an interval of 60 secs. before the chamber was illuminated and the presentation initiated by the experimenter throwing a switch.

When the IPI for any subject was 0 secs., a single long stimulus presentation was given. This was terminated manually by the experimenter after 19mins. had elapsed from the beginning of the presentation.

10.2 Method of Analysis

Analysis of results will be in terms of:

a) The gross effect of IPI on mean amount of each behaviour per session.
b) The effect of IPI on the course of behaviour over successive presentations within the sessions.

10.2 (a) Gross Effects

The mean amount of each behaviour of interest was

calculated over successive presentations, giving a mean for the entire session at that IPI. This was performed for every subject and the significance of the effect of IPI on mean amount of the behaviour per presentation was tested by applying a Friedman 2-way analysis of variance over IPI's (df = 4). In addition, the mean amount of behaviour at each IPI was compared with the mean amount at every other IPI (paired comparisons). Significance testing was by Wilcoxon Matched-Pairs signed ranks test.

If a significant effect of IPI on the duration of a behaviour is found, this can be due to 3 possible factors.

1. The frequency of the behaviour could have changed, but each of its individual occurrences (bout lengths) could remain of the same mean duration.
2. The frequency of the behaviour could remain unchanged but its mean bout length could have changed, thus producing an increase in total duration.
3. Both frequency and mean bout length could change together to produce a change in duration due to both factors.

Because the factors causing the onset of a behaviour (frequency) and those causing persistence in that behaviour (bout length) may not be the same, it is important in the context of this analysis that they be distinguished. For this reason, for the two behaviours whose duration is of interest in this experiment (Bu(d) and LD(d)) analysis of frequencies and mean bout lengths will be carried out to determine the source of IPI effects. The mean bout length of a behaviour in this analysis was calculated by dividing total duration by total frequency for the entire session, not by computing the mean of the mean bout lengths for individual presentations. This latter procedure could include bout lengths of 0 secs. which would lead to an underestimate of mean bout length. When the mean bout length of a behaviour is referred to, the letter "b" in

parentheses will be appended to the behaviour name abbreviation. For example, LD(b) means lateral display mean bout length.

10.2 (b) Effects Over Successive Presentations

This analysis attempted to detect differences in the course of behaviours over successive presentations due to different IPI's. For each IPI the mean amount of the relevant behaviour was calculated for successive presentations. Testing for significant non-stationarity was by Friedman 2-way analysis of variance. To allow visual comparison of differences in non-stationarity due to IPI, some smoothing of the data was required. This was accomplished by expressing the mean amounts of behaviours (over subjects) for successive presentations as a moving average based on successive batches of 5 presentations. This involved the computation of a grand mean for presenatations 1-5, 2-6, 3-7, 4-8...26-30. The representation of the course of a mean amount of a behaviour as a moving average allows data from all IPI's to be presented together.

Bout length analysis was not carried out for within session changes in behaviour because all the behaviours investigated in this experiment failed to occur during some presentations in some subjects.

10.3 Gross Changes in Attack - Results

10.3 (a) Biting

Fig. 39 shows the mean number (over subjects) of bites per presentation produced in sessions of each interpresentation interval (IPI). It can be seen from these that the mean number of bites increased from IPI(0) to IPI(1) and declined thereafter approximately to a negative exponential function of IPI. The change in mean bites with changes in IPI was

significant over all IPI's (Friedman, $p<.001$), and Table 22 shows the significances of the differences when comparisons are made between every IPI and every other (Wilcoxon). From these pair comparisons it can be seen that IPI(1) produces significantly more bites than IPI(0), (Wilcoxon, $p<.05$).

10.3 (b) Butting Frequency

Fig. 40 shows the mean number of butts per presentation at each IPI. As with biting there was an increase in mean frequency from IPI(0) to IPI(1) and thereafter a decline. The change in butting frequency with change in IPI was significant (Friedman, $p<.001$). Comparisons between IPI pairs (Table 23) reveal that only the differences between IPI(70) and all other IPI's except IPI(30) were significant.

That the decline in Bu(f) from IPI(1) to IPI(70) is not negative exponential in form is attributable to an unusually large number of butts emitted by a single subject at IPI(30). If median Bu(f) is considered (Fig. 41), the decline from IPI(1) to IPI(70) more closely resembles a negative exponential function.

The results of comparisons between every IPI and every other are shown in Table 23. The difference in butting frequency between IPI(0) and IPI(1) was not significant (Wilcoxon, $p>.05$)

10.3 (c) Butting Durations

Fig. 42 shows that the mean butting duration per presentation decreases from IPI(0) to IPI(70). Median butting duration, however, (Fig. 41) shows an increase from IPI(0) to IPI(1) and thereafter a decline approximating

to a negative exponential function. The change in butting duration with IPI is significant (Friedman, $p<.01$). Paired comparisons between IPI's (Table 24) reveal that only IPI(0) and IPI(70) and IPI(1) and IPI(70) differ significantly (Wilcoxon, $p<.02$ and $p<.02$ respectively).

10.3 (d) Butting Mean Bout Length

Fig. 43 shows that the mean bout length of butting decreased from IPI(0) to IPI(70). However, the median of the mean bout lengths represented in Fig.41, shows an increase from IPI(0) to IPI(1) and thereafter shows a decrease. The overall change in mean bout length was significant (Friedman, $p<.01$) and paired comparisons (Table 25) show that IPI(0) and IPI(1) did not differ significantly (Wilcoxon, $p>.05$).

10.3 (e) Discussion

All attack behaviours decrease in frequency when the IPI is increased from 1 sec. to 70 secs. Only biting shows a significant increase in mean frequency from IPI(0) to IPI(1), but median butting frequency, duration and mean bout length show a nonsignificant pattern in the same direction. Butting duration and mean bout length are affected by increase in IPI from 0 secs. to 70 secs. in a manner similar to biting and butting frequency. This and the high positive correlations found in ch. 8.3 between biting, butting frequency and butting duration, suggest that a single attack tendency is sufficient to account for all overt attack behaviours. The present results suggest that this tendency depends for its state on the density of stimulus presentations in time. The shape of the curve relating the amount of attack behaviours to the intervals by which stimulus presentations are separated, suggests that the effects of stimulus presentations in stimulating attack

are cumulative and that this excitation decays between presentations. Thus with short interpresentation intervals, the increment in attack tendency produced by a presentation decays less before the next presentation occurs, than when IPI's are long. These results are in agreement with those of Heiligenberg (1964) for the effect of interuptions on attack in unrestrained cichlids (Pelmatochromis subcellatus kribensis).

It was earlier shown that during continuous aggressive encounters, the rate of biting increases. If this increase depends on the incrementing of the attack tendency by the presence of the rival, then the effect of increasing IPI should be to reduce this rate of increase. To test this, the course of attack over successive presentations at the various IPI's, was examined.

10.4 Changes in Attack Over Presentations - Results

10.4 (a) Biting

Figs. 44-48 show, in terms of mean number of bites per presentation, the course of biting during sessions at each IPI. At IPI(0) mean bites per presentation increased significantly over the session (Fried., $p<.001$). At IPI(1) biting also increased significantly but at a higher rate (Fried., $p<.001$). At IPI(10) the rate of increase was comparable to that at IPI(0) and also significant (Fried., $p<.001$). When IPI was increased to 30 and 70 secs. the increase in mean biting was not significant (Fried., $p>.30$ and $p>.50$ respectively).

Fig.48.1 shows the moving average of the mean number of bites per presentation at each IPI. From these it can be seen that the rate of increase in biting was highest for IPI(1), followed by IPI's 0, 10, 30 and 70 secs. Furthermore, at all IPI's, except perhaps IPI(10), biting frequency reached an asymptote towards the ends of sessions.

10.4 (b) Butting Frequency

Figs. 49-53 show the mean frequency of butting per presentation over sessions of each IPI. Significant nonstationarity occurred at IPI(0) (Fried., $p<.001$), IPI(1) ($p<.001$) and IPI(10) ($p<.001$), but not at IPI(30) ($p>.10$) or IPI(70) ($p>.10$).

Fig. 54 shows the moving average butting frequency over successive presentations at each IPI. The rate of increase was highest at IPI(1) followed by IPI's of 0, 10, 30 and 70secs. respectively. With the possible exception of IPI(70) the rate of increase in butting frequency declined towards the ends of sessions.

10.4 (c) Butting Duration

Figs. 55-59 show that mean butting duration per presentation increased significantly as sessions progressed at IPI(0) (Fried., $p<.001$), IPI(1) ($p<.001$), IPI(10) ($p<.001$) and IPI(30) ($p<.05$). No significant change over presentations was found at IPI(70) (Fried., $p>.20$).

In contrast to the results for biting and butting frequency, Fig. 60 shows that the moving average butting duration had its highest rate of increase at IPI(0) and progressively lower rates as IPI increases to 70secs. With the possible exception of IPI(10) butting duration reached an asymptote towards the ends of sessions.

10.4(d) Discussion

Over successive presentations of a displaying male conspecific, male Bettas increase the amounts of all attack behaviours. The rate at which this increase occurs is dependent on the duration of the inter-presentation interval. For the behaviours biting and butting frequency the highest rate of increase occurs at an IPI of 1 sec., followed by IPI's of 0, 10, 30, and 70 secs. The duration of butting however, increases most rapidly at an IPI of 0 secs. and

progressively less rapidly as IPI is increased. The mechanism underlying all attack behaviours may be such that each stimulus presentation produces an increment in the tendency to attack, and this increment tendency decays between presentations.

That the presentation of dummy fish showing appropriate markings will raise the rate of attack has been shown for *Haplochromis burtoni* by Heiligenberg, Kramer and Schulz (1972) and Leong (1969).

This excitation process continues to increase attacks for 2 - 4 mins. into the post-stimulatory period, after which time, attack declines to its pre-stimulatory level (half-time approx. 3mins.). The results of the present experiment may be accounted for by postulating a similar process controlling Betta splendens attack, but on a different time-scale. The increase in attack found to occur during 15mins. encounters (ch. 7.2(d)) may be caused by the incrementation of the attack tendency by the constant presence of the conspecific stimulus. When such an encounter is broken down into 30sec. presentations separated by different intervals, more attack occurs if the interval is very short (1 sec.) while fewer occur as the interval is increased to 70 secs. The gross difference in attack at different IPI's is due to differences in the rate at which attack increases over the session.

The effect of a presentation may then be to increment the attack tendency by a given amount. If the interval between presentation is 10 secs. or greater, then some of this increment has decayed by the time the next presentation occurs. By extrapolation from the curve relating bites per presentation to IPI, it could be seen that with an IPI of about 150secs. a session would produce very few bites, because stimulus presentation induced excitation would decay to such an extent before the next presentation that no cumulation of attack tendency would occur.

The reason for the increase in mean attacks per presentation when an IPI of 1 sec. is used may be that attack tendencies continue to increase for a short time after the presentation has ceased, and when the next presentation occurs, its effect is superimposed on a level of attack tendency higher than would have existed without the short interval.

The finding of an asymptote in the rate of increase in attack behaviours over presentations poses additional questions about the nature of the system controlling attack. Since this asymptote occurs even when the rate of attack is low (at high IPI's) it cannot be due simply to the existence of a ceiling on the amount of attack which can occur during a presentation. Instead, the system must include processes which can account for a change in the amount by which a single presentation increments attack. This could be accounted for by the postulation of several different kinds of processes of which only two will be considered here. The first would involve a relation between the amount of increment in attack tendencies that a presentation produces and the absolute level of the tendency before incrementation, such that the higher level of the tendency, the greater (according to some function) the amount of stimulation needed to raise it by a given amount. The second possible process does not involve the invocation of a change in the capacity of any particular amount of stimulation to produce any given increment in attack rate. Instead, as is implied by a negative exponential decay process, during inter-presentation intervals, the amount that a given level of attack decays in a given time before the next presentation, increases with the level of the tendency before decay. The apparent increment in attack produced by a presentation would therefore decline as the level of the tendency before incrementation increases. Whichever of these processes is operating to produce the observed asymptote in the rate of increase of attack, the phenomenon itself implies that not

only are successive presentations of a displaying rival not homogenous in the attack behaviour they elicit, but also that they are not homogenous in the change they produce in the behaviour elicited.

10.5 Gross Changes in Lateral Display

10.5 (a) Lateral Display Duration - Results

Fig. 61 shows the mean duration of lateral display per presentation in sessions of each IPI. Mean LD(d) decreased slightly from IPI(0) to IPI(1) and thereafter increased to IPI(70). The change over all IPI's was significant (Fried., $p<.01$). Table 26 shows the significances of the differences when comparisons are made between every IPI and every other. Mean lateral display durations at IPI's of 0, 1, 10 and 30secs. did not differ significantly from each other, but all differed significantly from IPI(70).

10.5 (b) Lateral Display Frequency

Fig. 62 shows the changes in mean LD(f) with changes in IPI. The overall effect of IPI was significant (Fried., $p<.01$). Mean LD(f) increased from IPI(0) to IPI(1), decreased slightly to IPI(10) and thereafter increased to IPI(70). LD(f) therefore behaved in response to IPI changes in the same way as LD(d) for all IPI's except IPI(1). The response of LD(d) to IPI(1) was to decrease slightly, while LD(f) increased. Paired comparisons of IPI's in terms of mean LD(f) are shown in Table 27. It can be seen that IPI(0), IPI(1) and IPI(10) did not differ significantly. All of these, however, differed significantly from IPI(70).

10.5 (c) Lateral Display Mean Bout Length

Table 28 shows that differences in LD(b) with changes in IPI were not significant (Fried., $p>.50$).

10.5 (d) Discussion

Lateral display duration increased significantly with increased IPI. This change was most marked when IPI was increased from 30 to 70 secs. The frequency of lateral display showed a similar effect of IPI, but no changes in the mean bout length of LD occurred. Because of this, the effect of IPI on Ld(d) must be attributed to the IPI effect on the frequency of that behaviour.

These results suggest that the mean bout length of LD is not controlled in the same way as its frequency or duration. Furthermore, the investigation of the relations between reward elicited displays reported earlier (ch. 8.3) revealed that LD(d) and LD(f) were not positively related*. The reason for this is that although correlation methods SCor and PCor produced positive correlations between LD(d) and LD(f) (method PCor significant), method MCor produced a nonsignificant negative correlation. The reason for this is not immediately obvious but it does mean that despite the similar effect of IPI on the frequency and duration measures of LD, these cannot be assumed to be similarly controlled. This is further supported by the difference between LD(d) and LD(f) in their relations* with operant latency. Only LD(d) showed a positive relation*.

10.6 Changes in Lateral Display Over Presentations - Results

10.6 (a) Lateral Display Duration

Figs. 63-67 show, in terms of mean LD(d) per presentation, the course of LD(d) over successive presentations at each IPI. At all IPI's, a significant decrease in LD(d) occurred being most abrupt in the IPI(1) condition. Inspection of mean LD(d) for the first presentation at each IPI reveals that mean LD(d) for IPI(70) started at a considerably

higher level than for other IPI's. Table 29 shows that this difference was not, however, significant (Fried., $p>.10$).

Fig.68 shows the moving average of mean LD(d) over presentations. At all IPI's, the rate of decline of LD(d) is fastest over the first 15 presentations. Towards the ends of sessions, LD(d) for all IPI's but IPI(70) reached approximately the same level (5-7 secs. per presentation). The level of LD(d) for IPI(70) remained at the end of sessions well above that for other IPI's.

10.6 (b) Lateral Display Frequency

Figs. 69-73 show, in terms of mean LD(f) per presentation, the course of LD(f) over successive presentations. The effect of IPI on LD(f) seems more complex than on any of the behaviours considered so far. For IPI(0), a steady nonsignificant decline in mean LD(f) occurred (Fried., $p>.50$). With IPI(1) there was some indication of an increase in mean LD(f) at the beginning of the session, but this effect was not significant (Fried., $p>.70$). With IPI(10), an initial increase in LD(f) was also evident and was followed by a decline. This nonstationarity was significant (Fried., $p<.05$) and the pattern of FD(f) over presentations involved first an increase followed by a decrease which was slower than for IPI(10). For IPI(70) a slow increase in LD(f) over the first 12 presentations was followed by an equally slow decrease. This effect was not significant (Fried., $p>.50$).

Fig. 74 shows the moving average mean FD(f) over presentations (from presentation 5). Differences between IPI conditions concerns the level which LD(f) had reached over the first 5 presentations and the degree to which it declined afterwards. Low IPI's (0 and 1) produced little initial increase and little subsequent decrease. Higher IPI's (10 and 30) produce a sharper initial increase and a steeper subsequent decrease. These are the IPI's producing

significant non-stationarity. The highest IPI used (IPI 70), resulted in a slow increase, then a slow decrease, LD(f) never falling to the levels reached with shorter IPI's.

10.6 (c) Discussion

Lateral display duration decreases significantly into sessions at all IPI's. As IPI is increased, the rate of decrease of LD(d) becomes more gradual. For LD(f) the effect of increasing IPI is to induce an inverted u-shape in LD(f) over presentations. This pattern of increase - decrease was significant only for the middle range of IPI's (10 and 30). The general level of LD(f) is highest at IPI(70) because it increases (slowly) to the highest level and thereafter declines to only a little less than its initial level.

The previous analysis showed that the change in lateral display duration with change in IPI could be explained by the change observed in lateral display frequency. The question was then raised as to how this could be so, when an earlier analysis had not found a positive relation* between these measures of lateral display. The present investigation of the patterns of LD(d) and LD(f) over presentations suggests, however, how these behaviours might be found to be unrelated. It must be pointed out that the reason for the failure to find a positive relation between LD(d) and LD(f) was because a single correlation method (MCor) produced a very low negative correlation (ch. 8.3(c)). Method PCor produced a significant positive correlation.

Method MCor correlated the mean (over subjects) of LD(d) and LD(f) over the 30 rewards observed. The present analysis showed that the changes over presentations in LD(f) only resemble those in LD(d) towards the later parts of sessions. Over the first few presentations at medium IPI's and for longer than this at IPI(70). LD(d) decreases

while LD(f) increases. Positive and negative relations between LD(d) and LD(f) would therefore coexist in the population on which a correlation could be based. Because of this, which of the two correlation methods MCor and PCor were used might markedly affect the sign and significance of the result.

The results of the present analysis indicate that although changes in LD(f) can account for the gross change found in LD(d), the differences in the effect of IPI on the course of these measures over presentations, indicates that not all duration changes occurring can be explained by changes in frequency.

The control of lateral displays may be more complex than the control of attack behaviours. Attacks can be accounted for by an excitation-decay process, with the underlying tendency being incremented by stimulus presentations, continuing to increase for a time after presentation and thereafter decreasing as a negative exponential function. The control of lateral display, however, may be different for frequency and duration measures, at least for the first few presentations of a series, and these measures are not similarly related* to operant latency. In common with attack behaviours the level of lateral display depends on the inter-presentation interval, its response to increases in IPI being to increase, while attack decreases.

10.7 Gross Changes in Air Gulping Frequency

10.7 (a) Results

Table 30 shows the effect of IPI changes on air gulping frequency. No significant nonstationarity was found (Fried., $p > .70$).

10.7 (b) Changes in Air-Gulping Frequency Over Presentation

Figs. 75-79 show the courses of AG(f) within sessions at the various IPI's. Significant non-stationarity was not found for any IPI but for some there appears to be a tendency to show an increase over presentations. Furthermore, AG(f) has been implicated in the motivation of operant behaviour by using two methods which correlate over rewards (MCor and PCor). Since operant latency decreases over successive rewards, and is negatively correlated with AG(f), a positive correlation between mean AG(f) and the serial position of the presentation would be expected in the present experiment. The Spearman correlations found are also presented in Figs. 75-79 which shows that IPI(1), IPI(10) and IPI(70) produce a significant positive correlation between AG(f) and presentation serial position. The difference between these and IPI's 0 and 30 seems to be that the latter produce a much sharper initial increase in AG(f) (from the first to the third presentation) after which AG(f) remains at a constant level. Those IPI's which produce a positive correlation between AG(f) and presentation serial position are those in which the increase in AG(f) to its steady level is more gradual. It must be pointed out, however, that the IPI's used in this experiment did not cover the entire range of inter-reward intervals which occurred in the operant experiments reported earlier. The possibility does therefore exist that IPI's longer than 70secs. might significantly affect AG(f).

10.7 (c) Discussion

No effect of IPI on the gross amounts of air-gulping was found and no significant non-stationarity existed within sessions at any IPI. Some evidence for an increase in mean air gulping frequency over successive presentations at some IPI's did however emerge. The reason for the differences

between IPI's in their effect on the correlations between mean AG(f) and presentation serial position is not clear.

Because of the lack of evidence for an IPI effect on AG(f) the control of this parameter of AG may not involve any excitory processes having decay functions detectable by the range of IPI's and the duration of presentation used in this experiment. Because of this, and the observation that mean AG(f) increases at all IPI's over the first few presentations of a session, AG(f) may simply be a breathing act and a measure of a general activity. This may be the case even when it has a considerable duration and a display-like form. AG(f) as simple breathing would also account for its positive relations with attack behaviours (ch. 8.3(c)), since these are vigorous activities. This hypothesis does not rule out the possibility that air gulping, and particularly extended air gulping, may also have a display function.

10.8 Reward-Elicited Behaviours and the Inter-Reward Interval

The experiment reported, manipulated the interval between presentations of an aggression-eliciting stimulus. By observation of the effects of those intervals on the gross amounts and intra-session patterning of behaviours earlier implicated in the control of operant behaviour, further conclusions can be drawn about this control and about the nature of the operant situation.

It was shown earlier (ch. 8) that biting, butting frequency and duration, and air-gulping frequency, were negatively related* to operant response latency. In addition it was found that lateral display duration was positively related* to operant response latency. These behaviours may control operant responding in that the motivational states underlying them may directly motivate or inhibit the operant response. However, the action of all of these behaviours except air gulping frequency could be explained by their

action on response-inhibiting post-reward behaviours. It was suggested that the relations* between operant latency and reward-elicited behaviours might have been found not because reward behaviours acted on operant responding, but because operant latencies (inter-reward intervals) determined the level of attacks and displays during rewards. This interpretation was rejected as a full account of the effects of reward behaviours because of their influence on post-reward behaviours.

The results of the present experiment indicate that of those reward elicited behaviours related* to operant latency only AG(f) is uninfluenced by changes in the intervals between stimulus presentations (for the IPI's sampled). These results have two implications:

1. The facilitatory relations* between AG(f) and operant latency may be due to a direct motivational link, in that it is not mediated by effects on post reward behaviours, and neither is it attributable to changes in the inter-reward interval. It is suggested that this behaviour is a measure of general activity level and will therefore determine and be determined by operant response rate.
2. Although the reward elicited behaviours Bi, Bu(f), Bu(d) and LD(d) do affect post-reward behaviours, and because of this their relations* with operant latency cannot be entirely attributed to their being themselves determined by operant latencies, the above experiment has shown that these reward-elicited behaviours are not independent of the interval between reward presentations. The dependence of these behaviours on the inter-reward interval means that the nature of the operant situation itself may be such that it interacts with certain aspects of the motivational system underlying reward.

Operant situations all involve some mininum inter-reward interval and this depends on such factors as the response-reinforcer distance and the reinforcement schedule being used.

Even if all reward elicited behaviours except AG(f) act on the operant responding only by acting on post-reward behaviours, any factor which increases the minimum inter-reward interval will affect operant responding. This will occur because increases in this interval will lower the level of attacks and will increase the duration of lateral display during rewards. These changes in reward-elicited behaviours will lead to an increase in the post-reward behaviours which will then more strongly inhibit the operant response. If reward-elicited motivational states act directly on the tendency to perform operant responses, as the relations between attack, the intention operant (Rf-Op) and frequency measures of search swimming (SeS(f)) and (SeS(d)) suggest, then the magnitude of the inter-reward interval will have an even greater effect on responding. As the minimum interval increases, so the tendencies to perform post-reward response-inhibiting behaviours will increase and the effects of reward in motivating the fish to perform the operant response will decrease.

Further assessment of the effects of reward-elicited behaviours on operant responding requires that reward behaviours should first be manipulated and the subsequent effect of those changes on operant responding be observed. Although this method cannot completely eliminate the effect of inter-reward interval, the finding that experimentally induced changes in display and attack are accompanied by changes in operant behaviour would further support the hypothesis that operant behaviour is controlled by reward-elicited behaviours or states. The following chapter reports an experiment involving such manipulation.

Figure 39

Mean number of bites (Bi) per presentation at each inter-presentation interval (IPI). N = 10.

IPI:	0	1	10	30	70
$\bar{X}$	1.12	1.51	1.04	.69	.42
SEM	.21	.31	.22	.21	.12
Total Ranks	36	43.5	33	21	16.5

Chi = 19.62

df = 4

p < .001

ω^2 = .4905

L = 511.5
p < .001

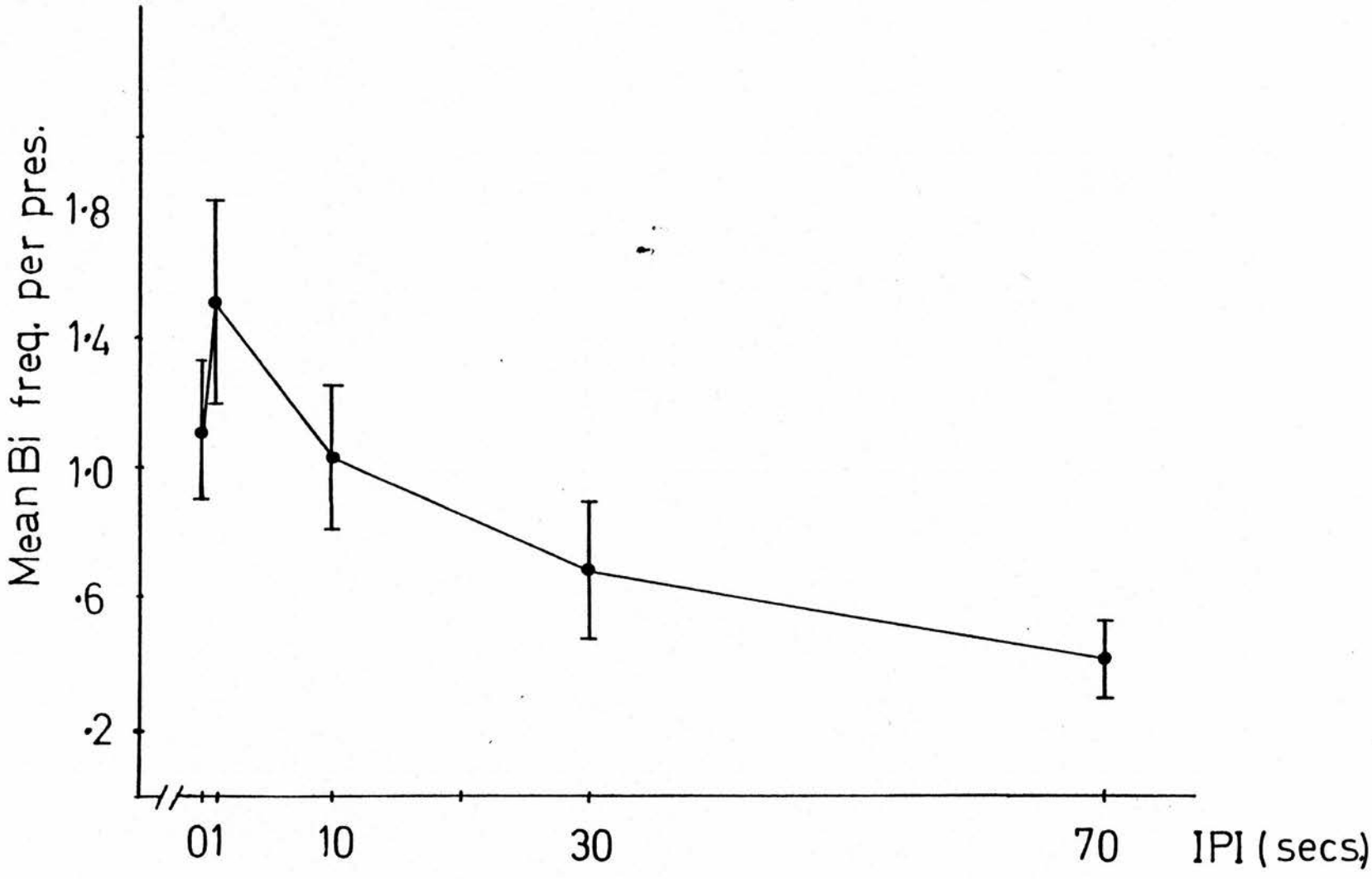

Mean Bi freq. per pres.
1·8
1·4
1·0
·6
·2
01
10
30
70
IPI (secs)

Figure 40

Mean butting frequency (Bu(f)) per presentation as a function of inter-presentation interval (IPI). Bars represent two standard errors. N = 10.

IPI	0	1	10	30	70
$\bar{X}$	1.88	2.14	1.53	1.41	.69
SEM	.40	.45	.43	.59	.15
Total Ranks	36	42.5	31	23.5	17

Chi = 16.18

df = 4

$p < .01$

$\omega = .4045$

$L = 508.5$

$p < .001$

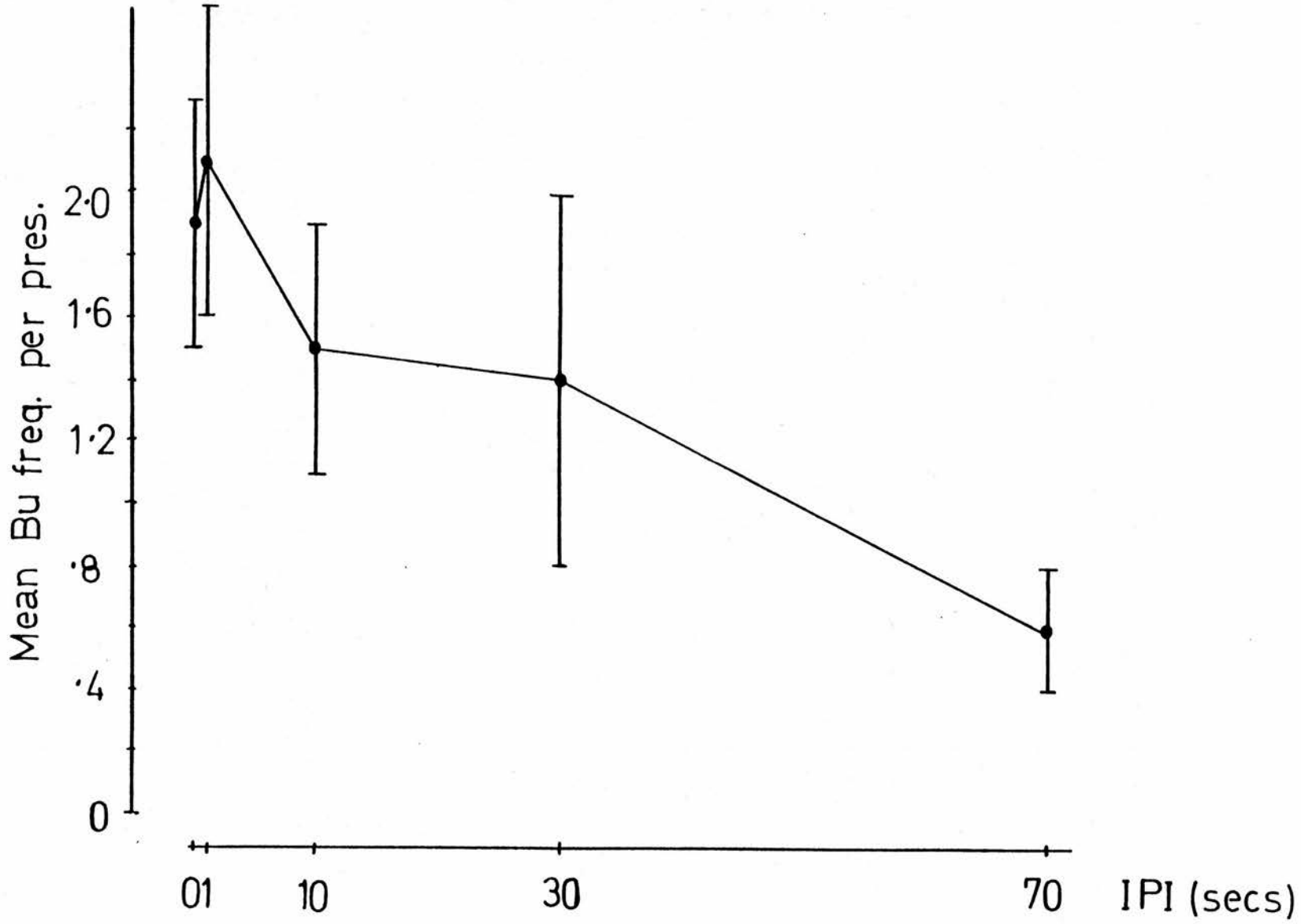

Mean Bu freq. per pres.
2·0
1·6
1·2
·8
·4
0
01
10
30
70
IPI (secs)

Figure 41

Median butting frequency, duration and mean bout length per presentation as a function of inter-presentation interval (IPI). N = 10.

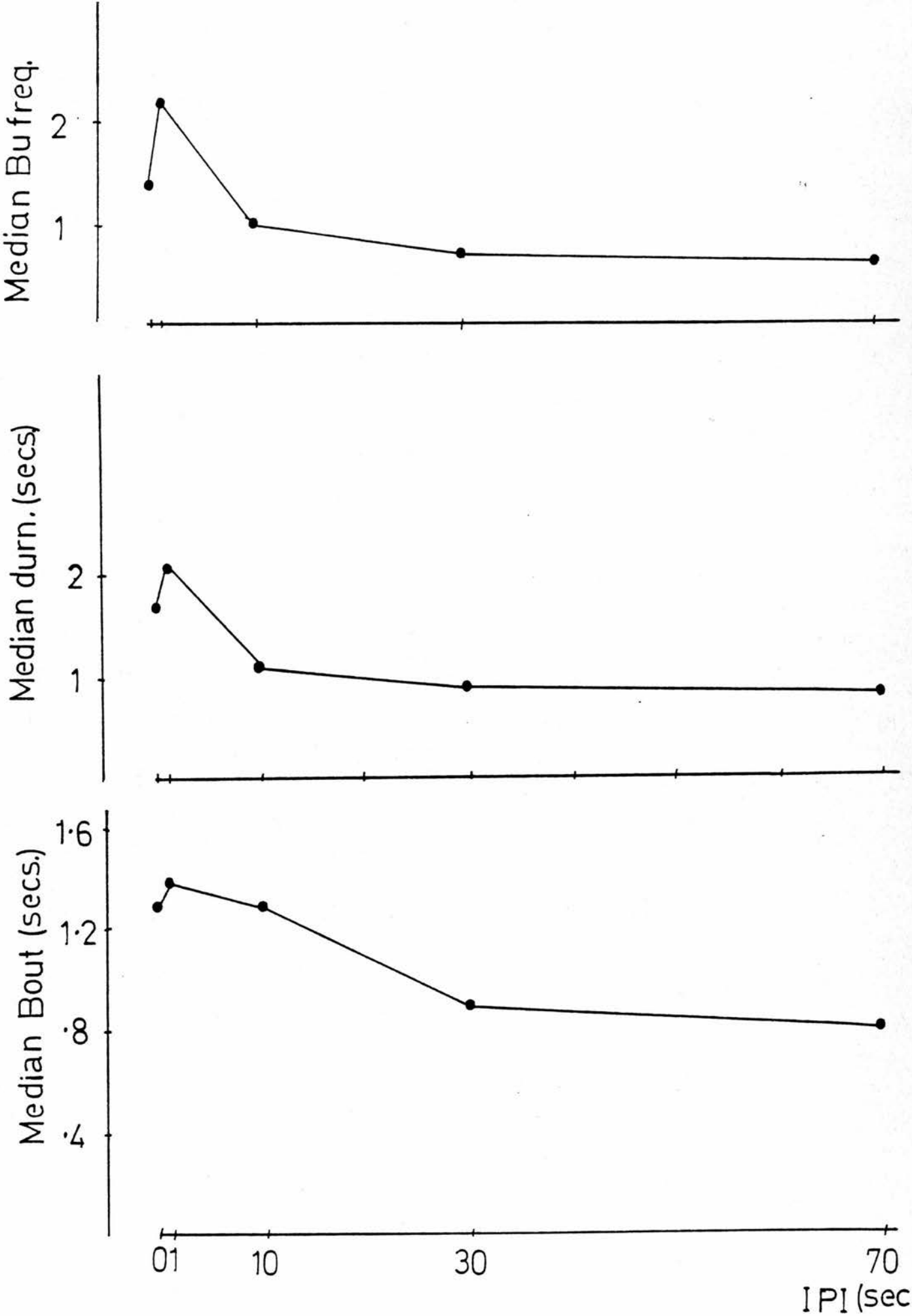

Median Bu freq.
2
1
Median durn. (secs)
2
1
Median Bout (secs.)
1·6
1·2
·8
·4
01
10
30
70
IPI (secs

Figure 42

Mean butting duration (Bu(d)) per presentation as a function of inter-presentation interval (IPI). Bars represent two standard errors. N = 10.

IPI	0	1	10	30	70
$\bar{X}$	4.2	3.6	3.2	2.3	.8
SEM	1.4	1.2	1.3	1.2	.2
Total Ranks	37.5	41.5	30.5	23	17.5

Chi = 15.76

df = 4

$p < .01$

$\omega = .394$

$L = 508.5$, $p < .001$

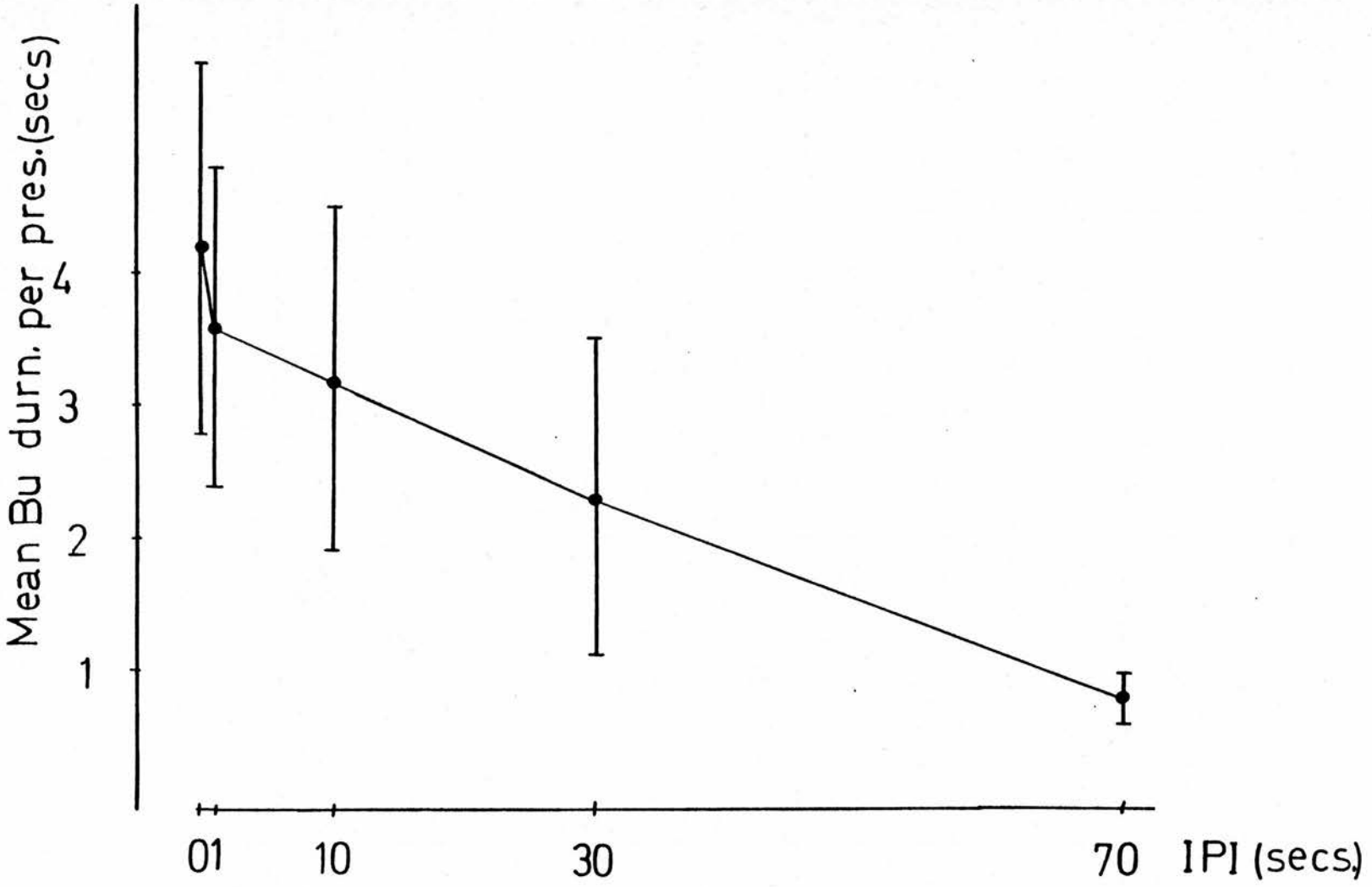

Mean Bu durn. per pres.(secs)
4
3
2
1
01
10
30
70
IPI (secs)

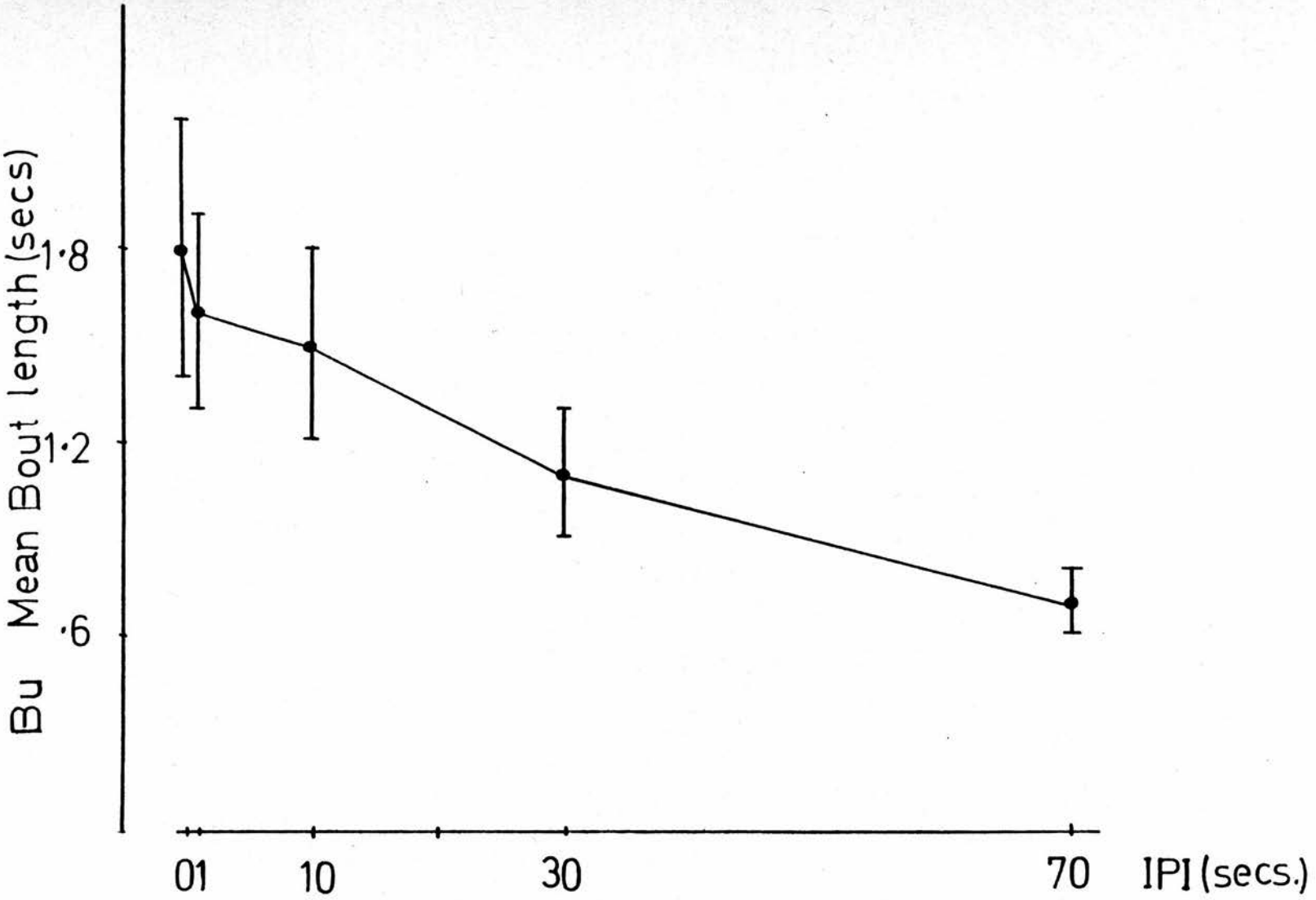
Figure 43

Butting (Bu) mean bout length as a function of inter-presentation interval (IPI). Bars represent two standard errors. N = 10.

	0	1	10	30	70 secs. IPI
$\bar{X}$	1.8	1.6	1.5	1.1	.7
SEM	.4	.3	.3	.2	.1
Total Ranks	39	40.5	32	21.5	17.0

Chi = 17.46
df = 4
$p < .01$
$\omega = .4365$

$L = 513$, $p < .001$


Bu Mean Bout length (secs)
1·8
1·2
·6
01
10
30
70
IPI (secs.)

Figures 44 - 48 (2 pages)

The mean bite (Bi) frequency during successive presentations at each inter-presentation interval (IPI) presentations. Bars represent two standard errors. N = 10.

Fig. 44 (Table 1, Appendix 1).

IPI(0) Chi = 79.2383 $L = 81861, p < .001$
df = 29
p < .001
ω .2732

Fig. 45 (Table 2, Appendix 1).

IPI(1) Chi = 75.9368 $L = 81966.5, p < .001$
df = 29
p < .001
$\omega = .2615$

Fig. 46 (Table 3, Appendix 1)

IPI(10) Chi = 70.5586 $L = 81047.5, p < .001$
df = 29
p < .001
$\omega = .2433$

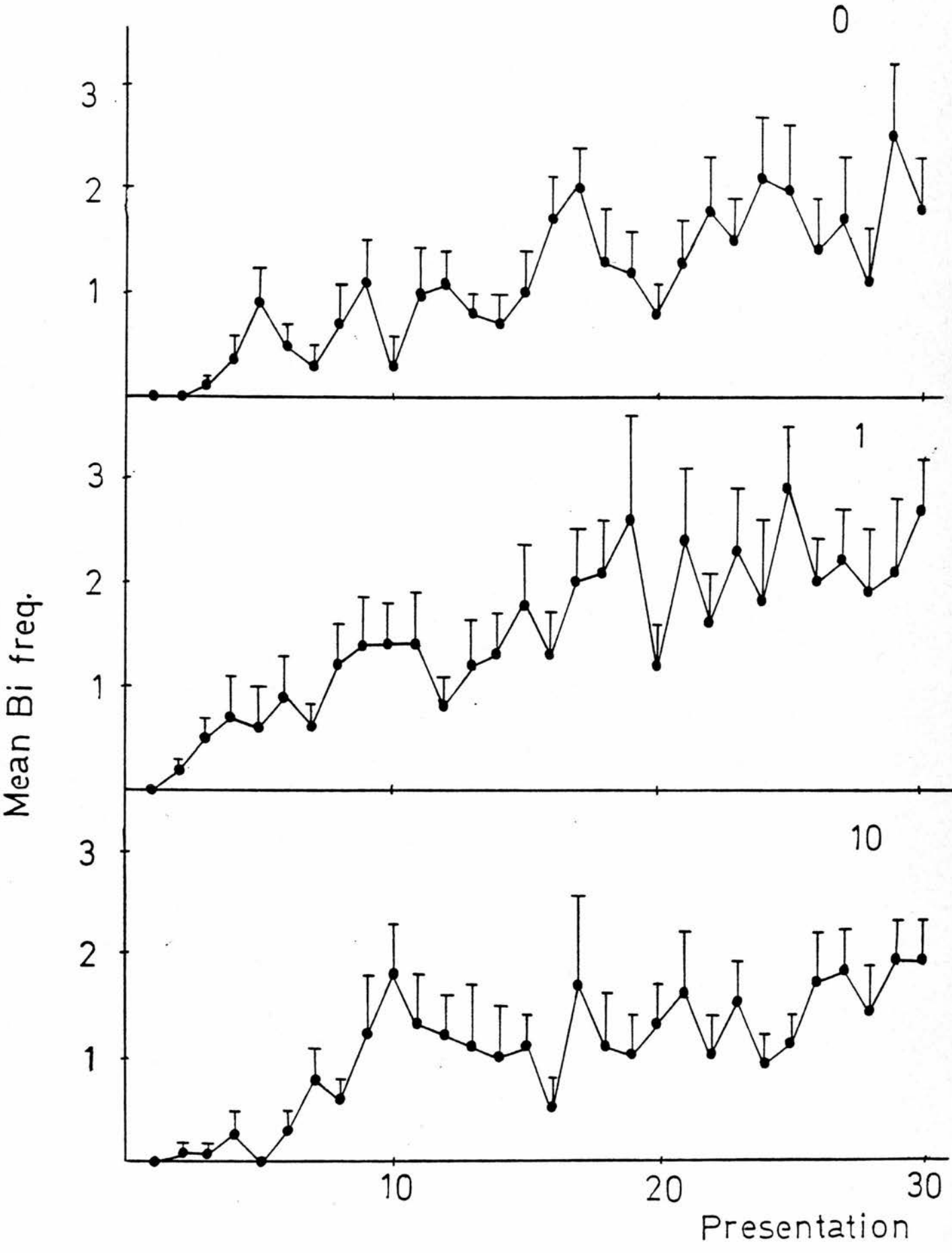

0
1
10
3
2
1
Mean Bi freq.
10
20
30
Presentation

Fig. 47 (Table 4, Appendix 1)

IPI(30) Chi = 32.2000
df = 29
N.S.

$\omega = .11103$

$L = 78015.5, p < .001$

Fig. 48 (Table 5, Appendix 1)

IPI(70) Chi = 27.3877
df = 29
N.S.

$\omega = .0944$

$L = 76581, p < .001$

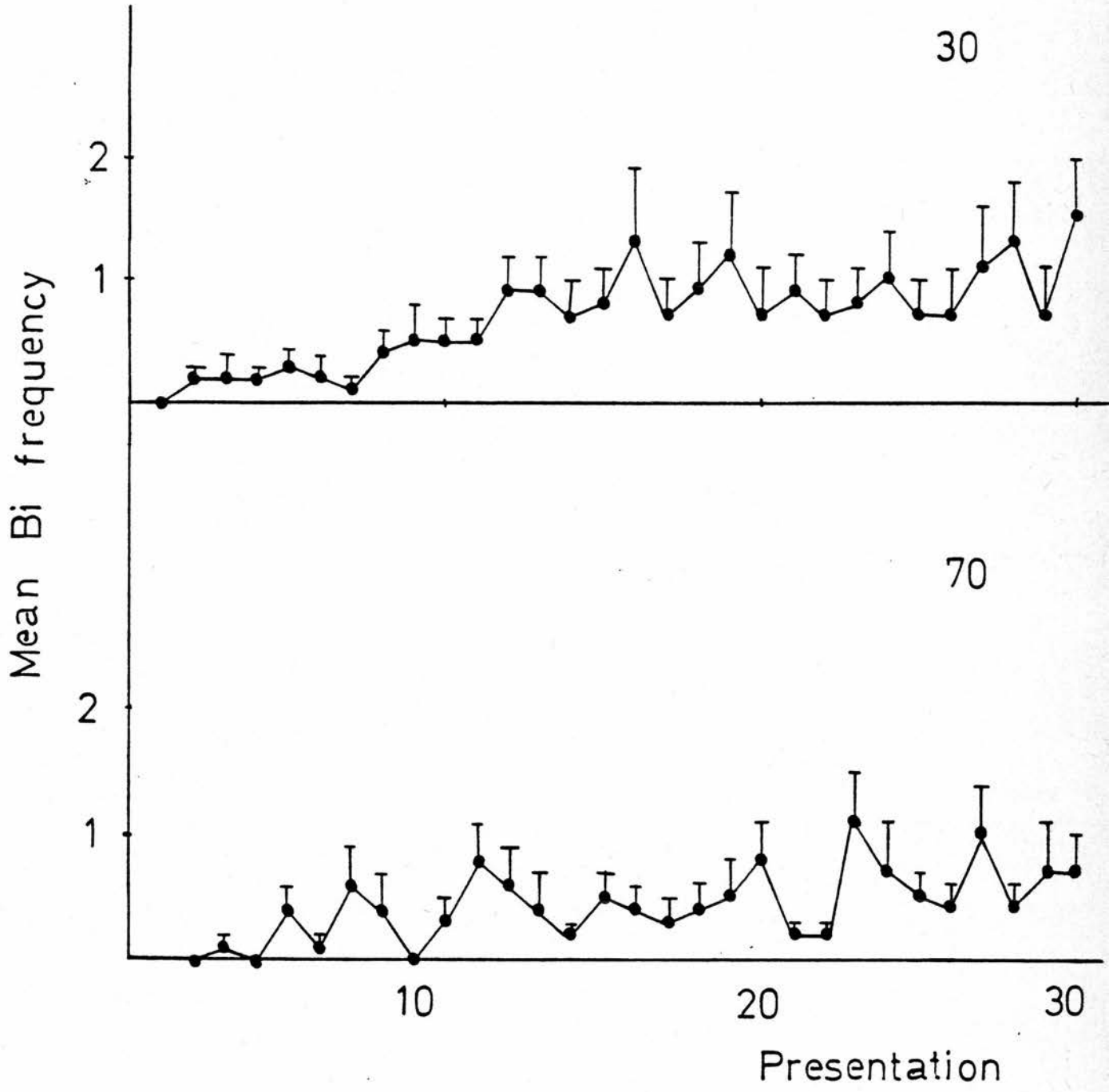
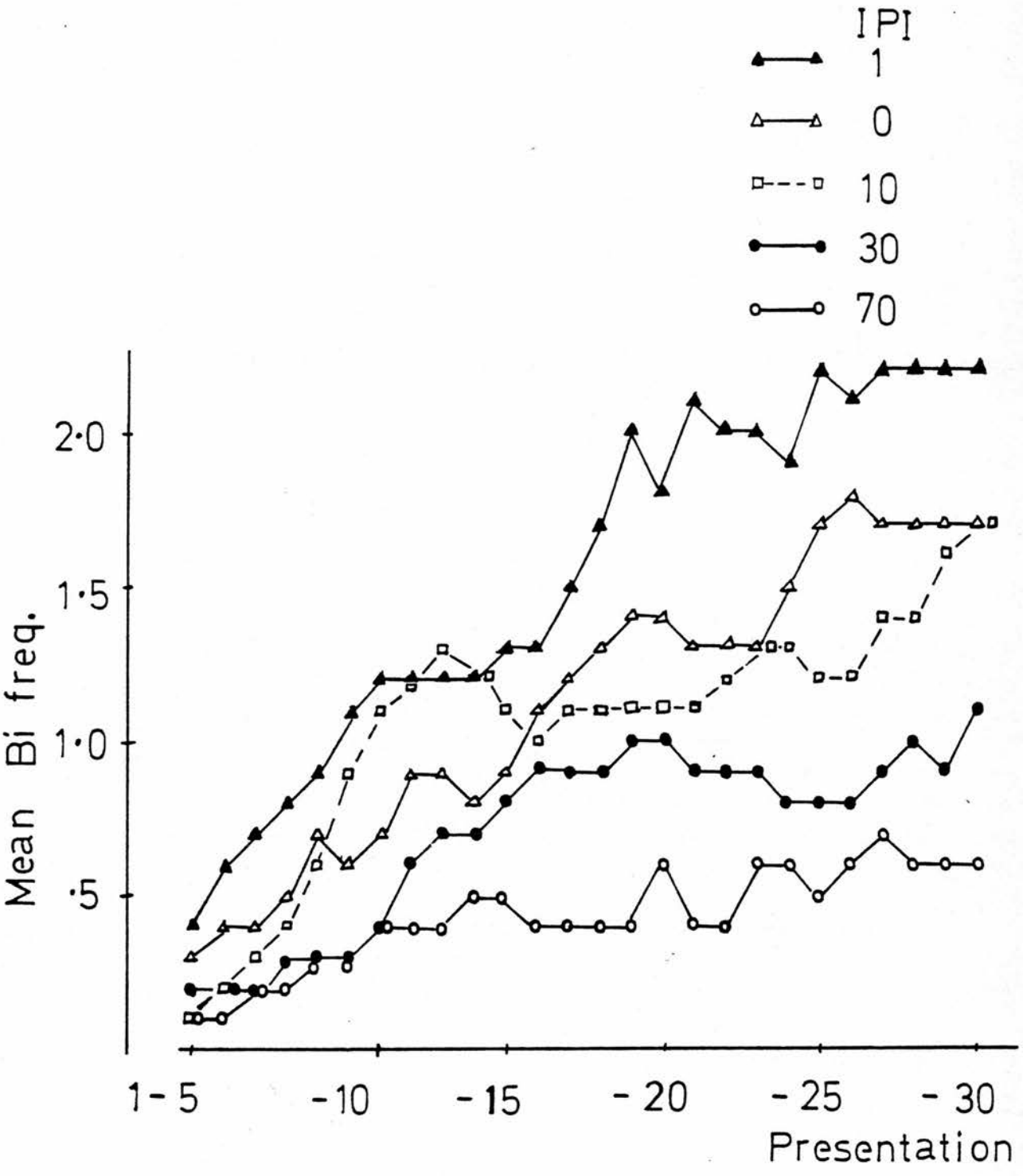

30
2
1
Mean Bi frequency
70
2
1
10
20
30
Presentation

Figure 48.1

The moving average biting frequency (Bi) for successive batches of 5 presentations at each inter-presentation interval (IPI).


IPI
1
0
10
30
70
2·0
1·5
1·0
·5
Mean Bi freq.
1-5
-10
-15
-20
-25
-30
Presentation

Figures 49 - 53 (2 pages)

Mean number of butts during successive presentations at each inter-presentation interval (IPI). Bars represent one standard error.

Fig. 49 (Table 1, Appendix 2)

IPI(0)

Chi = 73.7244
df = 29
p < .001
ω = .25422

L = 81074·5, p < .001

Fig. 50 (Table 2, Appendix 2)

IPI(1)

Chi = 84.4277
df = 29
p < .001
ω = .28773,

L = 82519·5, p < .001

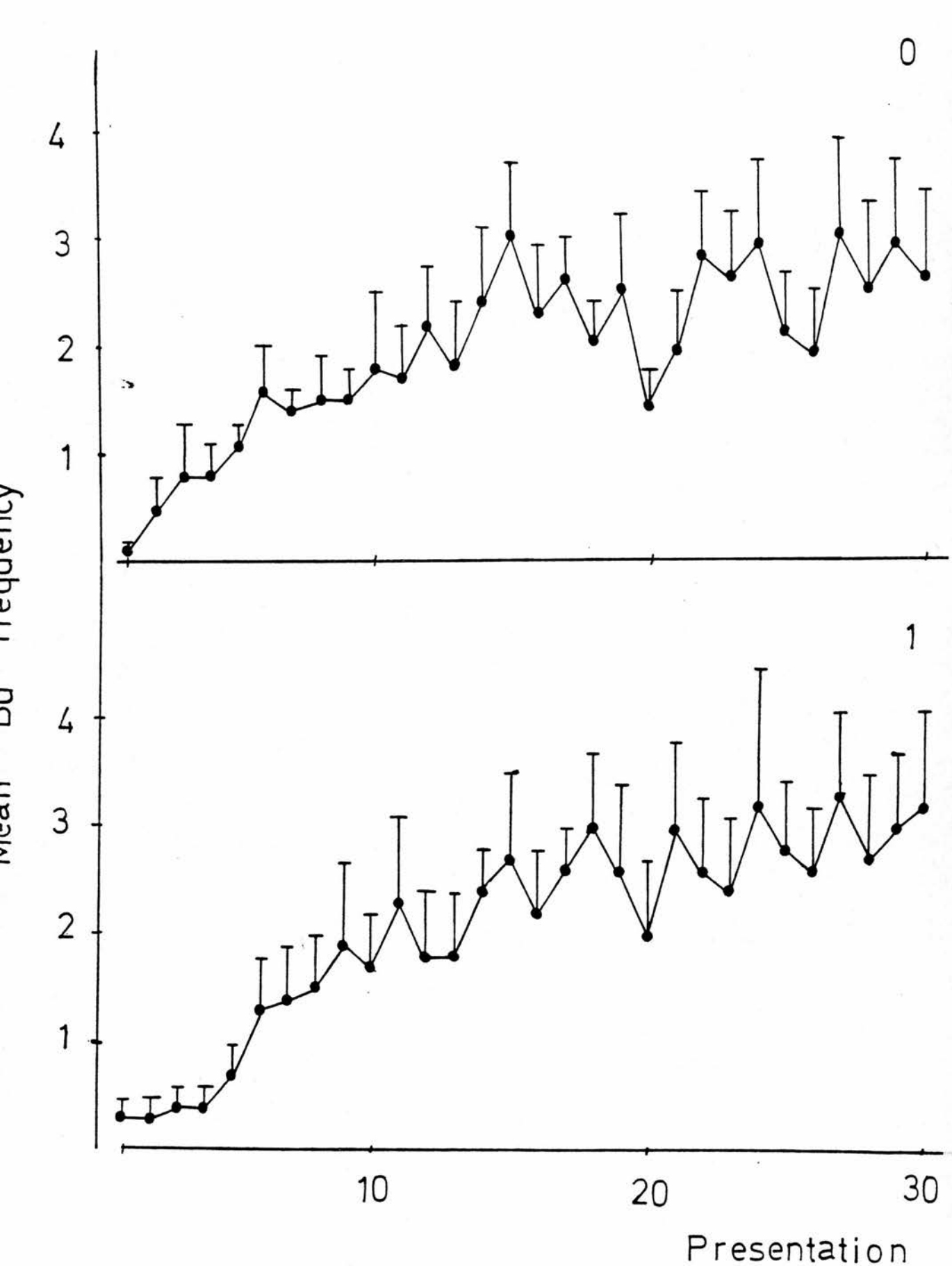

0
4
3
2
1
1
4
3
2
1
Mean BU Frequency
10
20
30
Presentation

Fig. 51 (Table 3, Appendix 2)

IPI(10) Chi = 65.3677 $L = 80336.5, p < .001$
df = 29
$p < .001$
$\omega = .2254$

Fig. 52 (Table 4, Appendix 2)

IPI(30) Chi = 37.5720 $L = 78889.5, p < .001$
df = 29
N.S.
$\omega = .13223$

Fig. 53 (Table 5, Appendix 2)

IPI (10) Chi = 38.1587 $, L = 77925, p < .001$
df = 29
N.S.
$\omega = .1316$

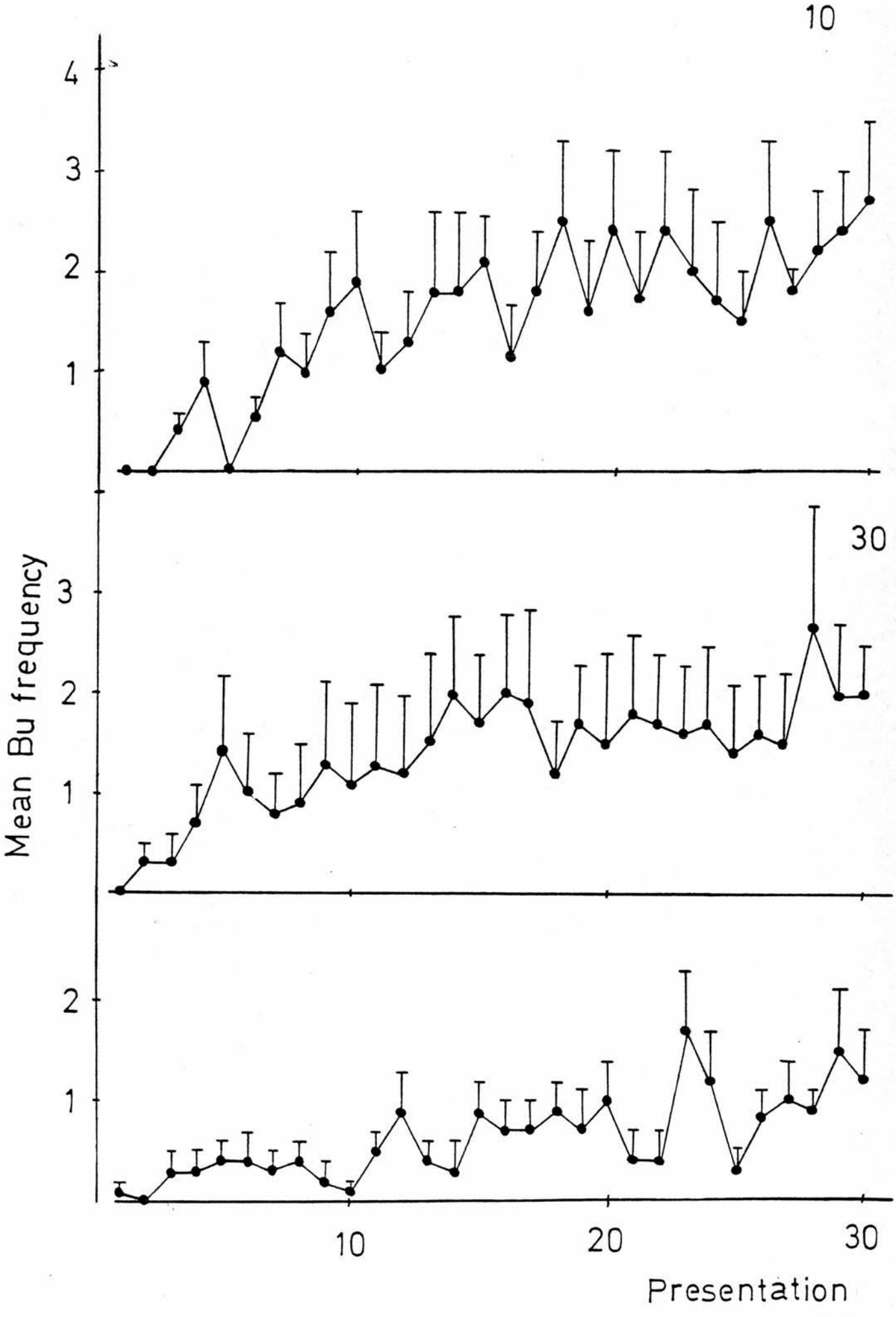
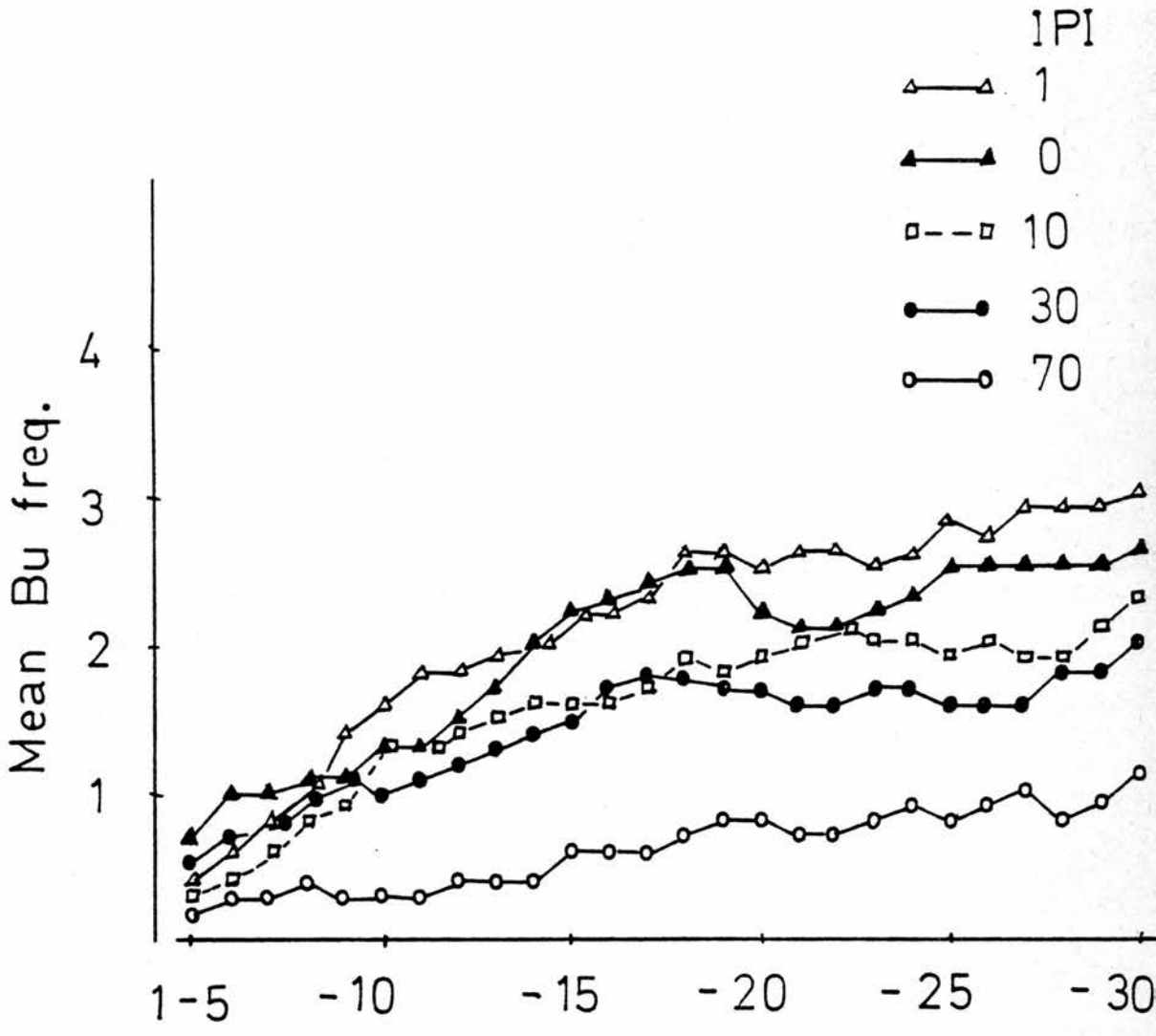

10
4
3
2
1
30
3
2
1
2
1
Mean Bu frequency
10
20
30
Presentation

Figure 54

The moving average butting frequency (Bu(f)) for successive batches of 5 presentations at each inter-presentation interval (IPI).


IPI
1
0
10
30
70
Mean Bu freq.
4
3
2
1
1-5
-10
-15
-20
-25
-30

Figures 55 - 59 (2 pages)

Mean duration of butting (Bu) during successive presentations at each interpresentation interval (IPI). Bars represent one standard error.

Fig. 55 (Table 1, Appendix 3)

IPI(0) Chi = 76.6528 $L = 81673.7, p < .001$
df = 29
$p < .001$
$\omega = .2639$

Fig. 56 (Table 2, Appendix 3)

IPI(1) Chi = 96.2671 $L = 83162, p < .001$
df = 29
$p < .001$
$\omega = .3320$

Fig. 57 (Table 3, Appendix 3)

IPI(10) Chi = 69.1929 $L = 80825.5, p < .001$
df = 29
$p < .001$
$\omega = .2388$

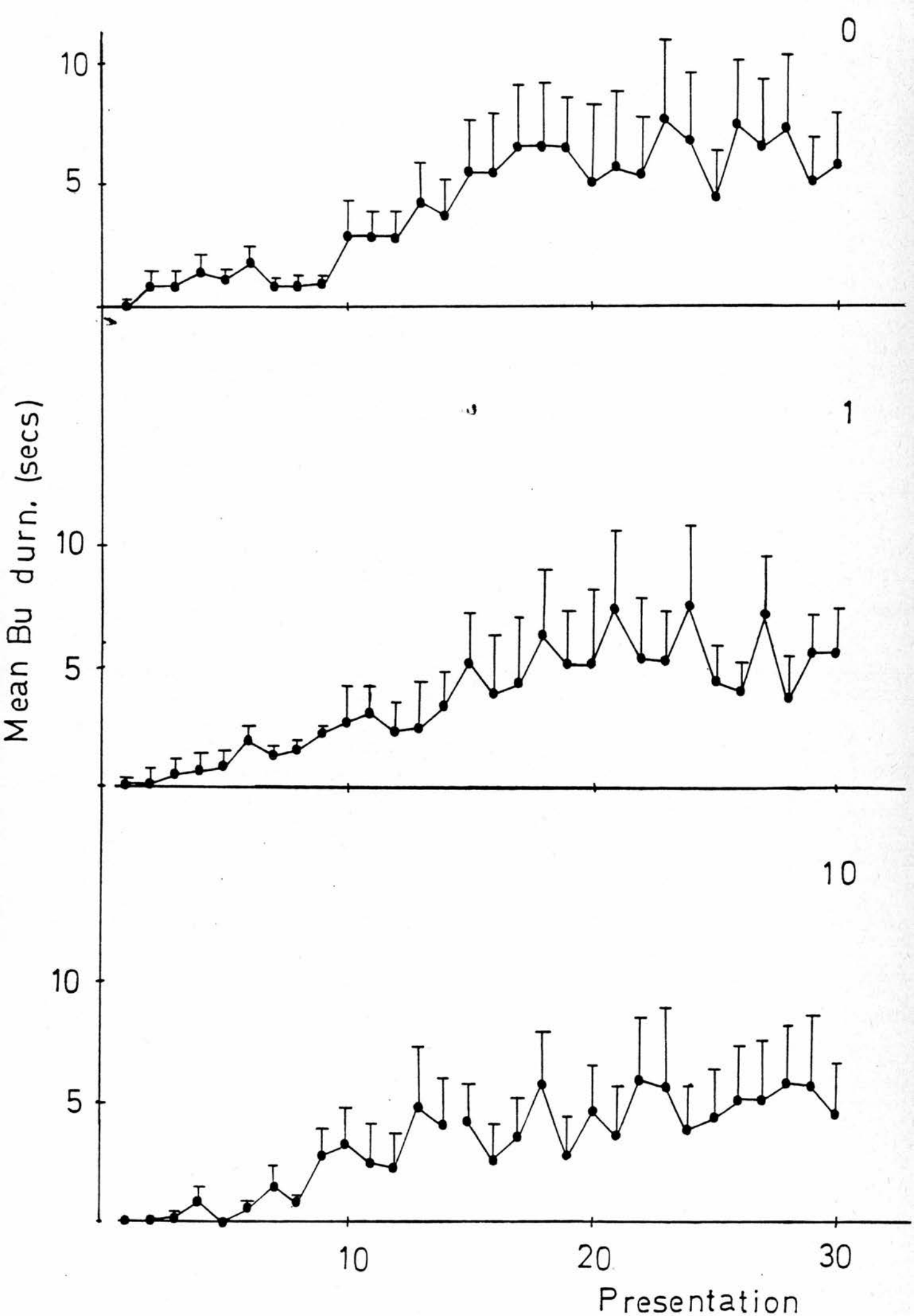

0
10
5
1
10
5
10
10
5
Mean Bu durn. (secs)
10
20
30
Presentation

Fig. 58 (Table 4, Appendix 3)

IPI(30)

Chi = 43.6875
df = 29
$p < .05$
$w = .15065$

$L = 79492.5, p < .001$

Fig. 59 (Table 4, Appendix 3)

IPI (70)

Chi = 33.5269
df = 29
N.S.
$w = .1158$

$L = 77605.5, p < .001$

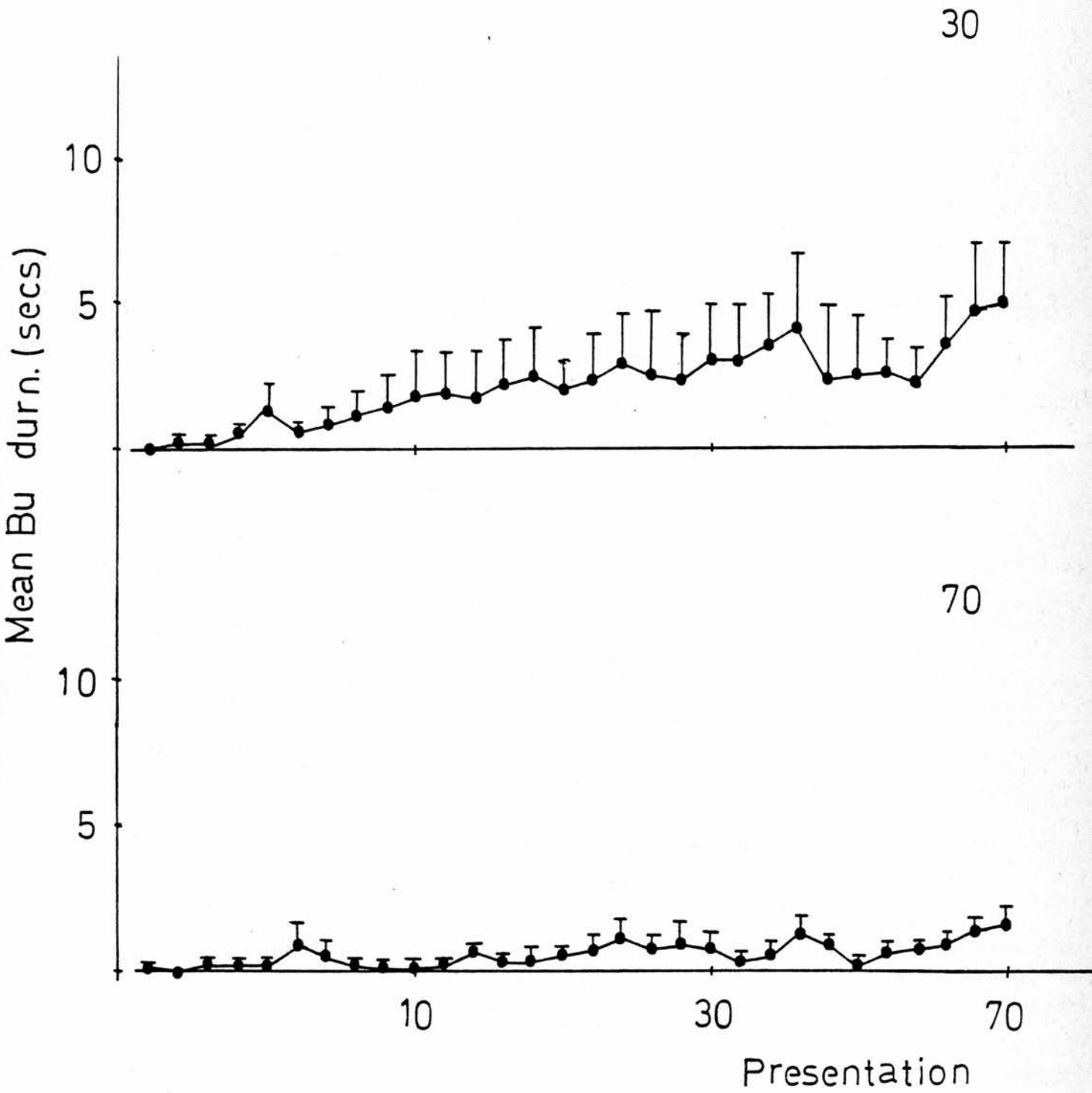

30
10
5
Mean Bu durn. (secs)
70
10
5
10
30
70
Presentation

Figure 60

The moving average butting duration (Bu(d)) for successive batches of 5 presentations at each inter-presentation interval (IPI).

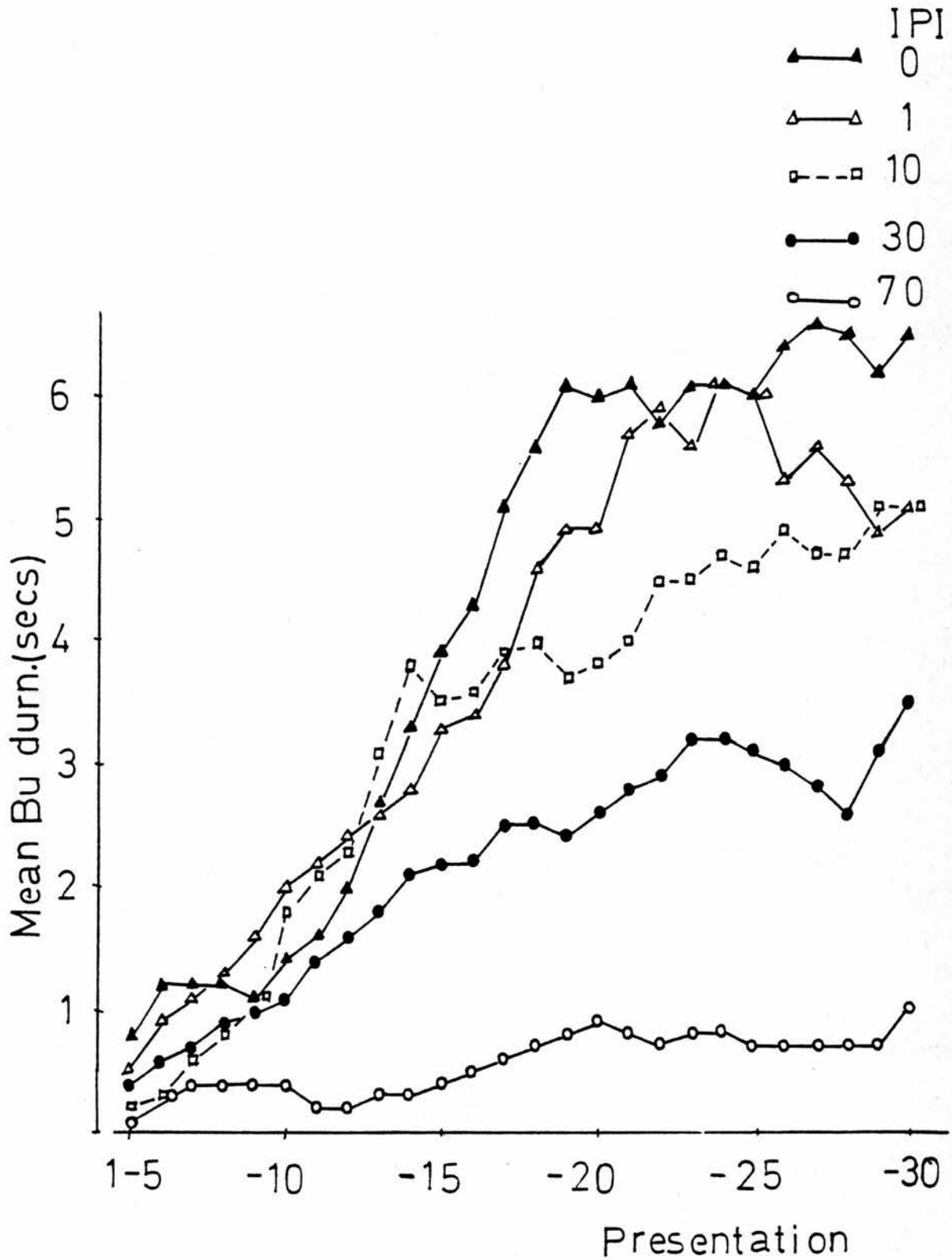

IPI
0
1
10
30
70
Mean Bu durn.(secs)
1
2
3
4
5
6
1-5
-10
-15
-20
-25
-30
Presentation

Figure 61

Mean lateral display duration (LD(d)) per presentation at each inter-presentation interval (IPI). Bars represent two standard errors. N = 10.

IPI	0	1	10	30	70
$\bar{X}$	7.2	6.9	7.8	8.1	10.7
SEM	1.7	1.4	1.2	1.2	1.1
Total Ranks	23.5	20.5	29	30	47

Chi = 16.90
df = 4
$p < .01$

$L = 506.5, p < .001$

$W = .4225$

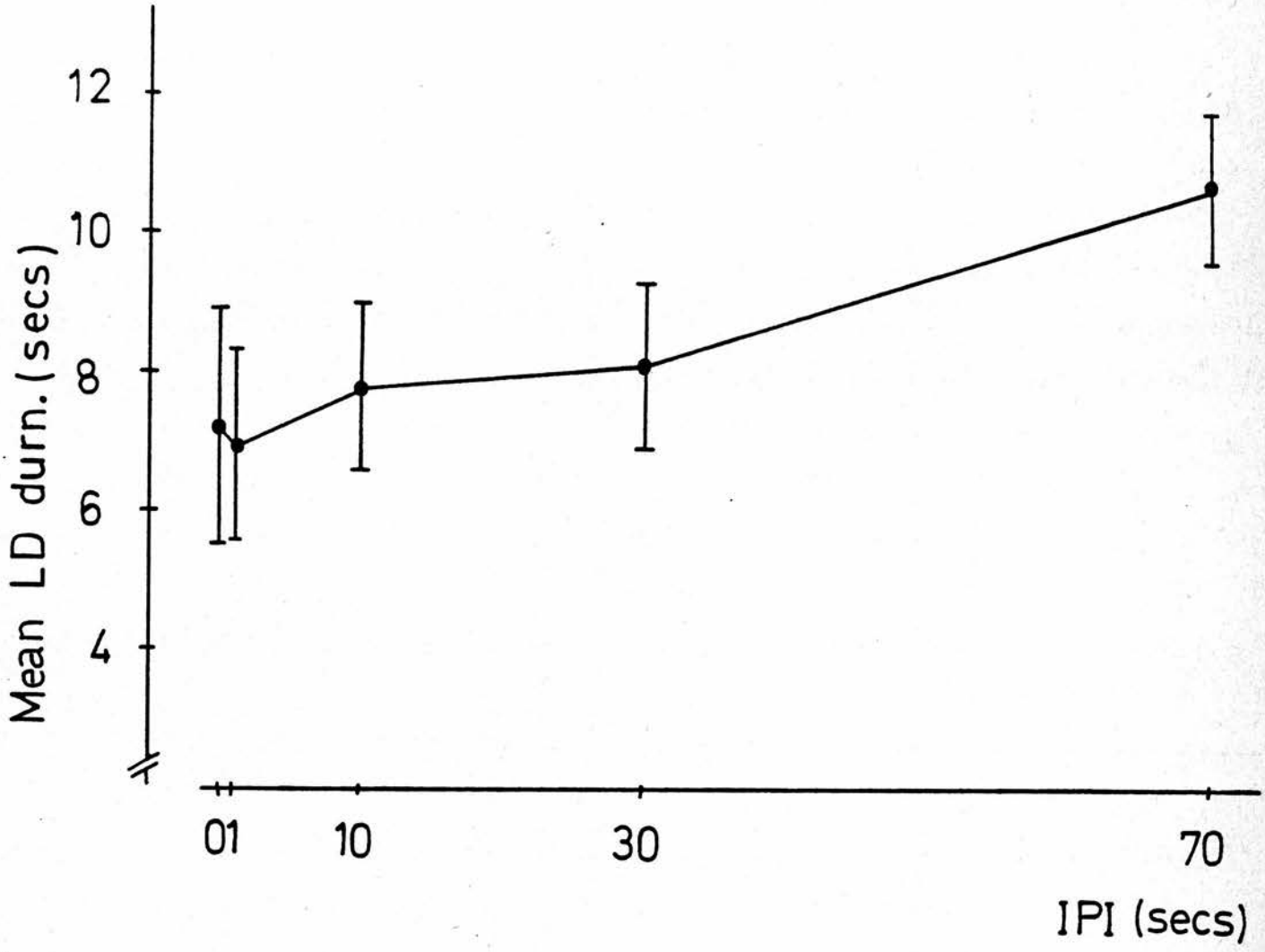

12
10
8
6
4
Mean LD durn. (secs)
01
10
30
70
IPI (secs)

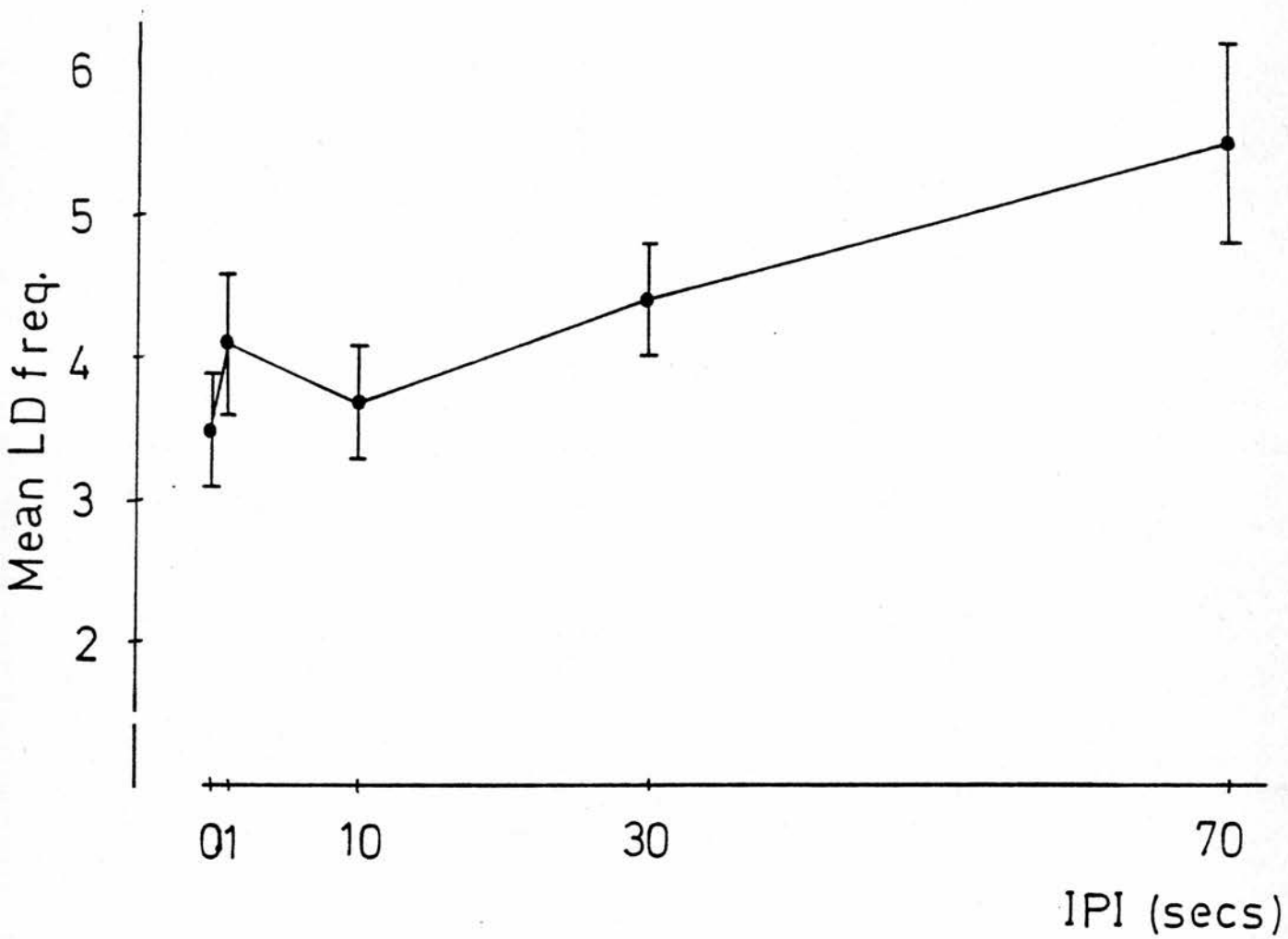
Figure 62

Mean lateral display frequency (LD(f)) per presentation at each inter-presentation interval (IPI). Bars represent one standard error. N = 10.

	0	1	10	30	70
$\bar{X}$	3.5	4.1	3.7	4.4	5.5
SEM	.4	.5	.4	.4	.7
Total Ranks	20.0	23.5	24	37	45.5

Chi = 18.70
df = 4
$p < .01$
$\omega = .4675$

$L = 514.5$, $p < .001$


Mean LD freq.
6
5
4
3
2
01
10
30
70
IPI (secs)

Figures 63 - 67 (2 pages)

Mean duration of lateral display during successive presentations at each inter-presentation interval (IPI). Bars represent one standard error. N = 10.

Figure 63 (Table 1, Appendix 4) IPI(0)

Chi = 56.9010
df = 29
p < .01
ω = .1859

L = 79253.5
P < .001

Figure 64 (Table 2, Appendix 4) IPI(1)

Chi = 47.2817
df = 29
p < .02
ω = .1611

L = 78510
P < .001

Figure 65 (Table 3, Appendix 4) IPI(10)

Chi = 58.6257
df = 29
p < .001
ω = .2023

L = 80766.5
P < .001

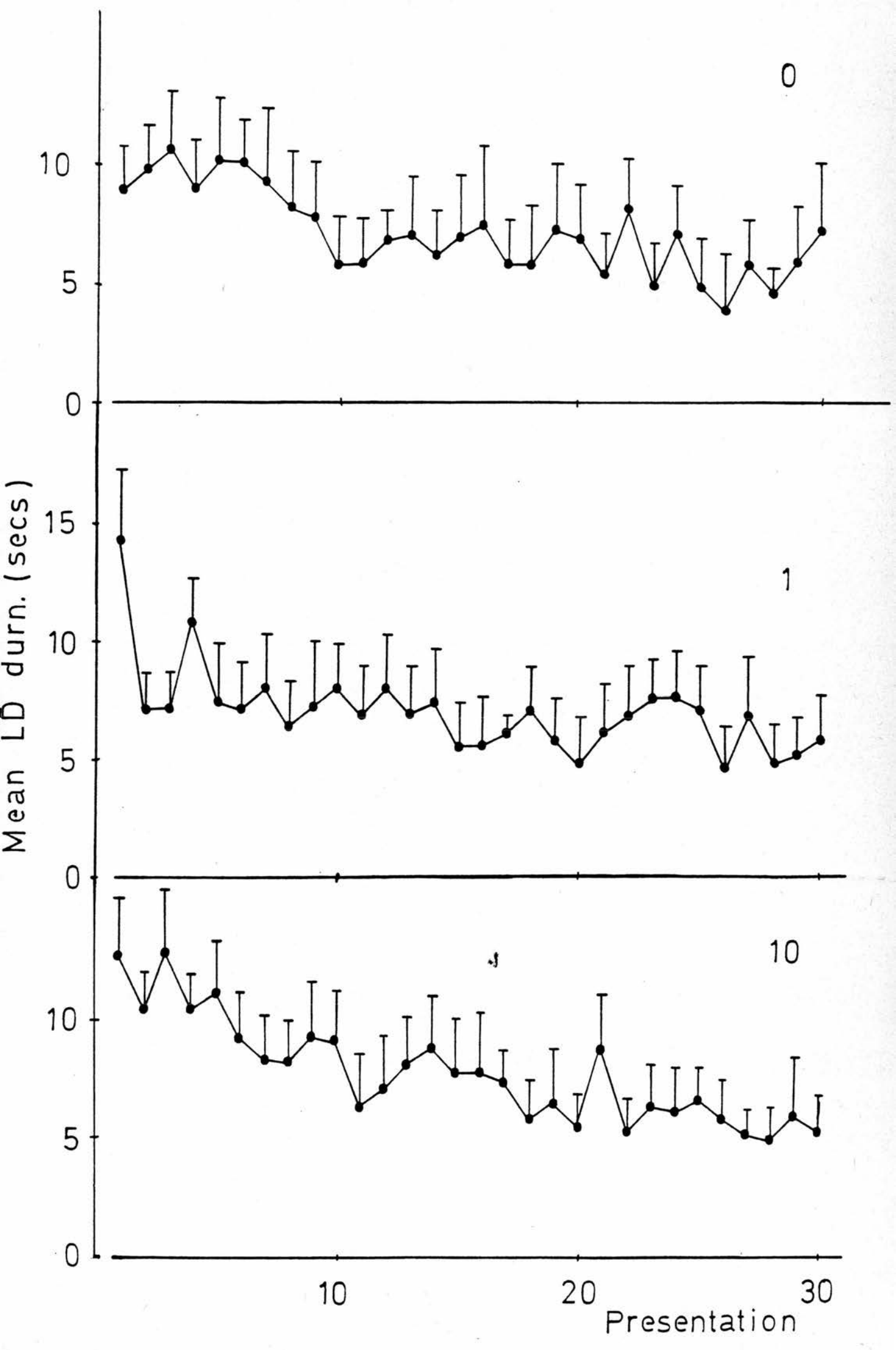

0
10
5
0
1
15
10
5
0
10
10
5
0
10
20
30
Presentation
Mean LD durn. (secs)

Figure 66 (Table 4, Appendix 4) IPI(30)

Chi = 73.5444
df = 29
p < .001
ω = .2536

L = 80593.5
p < .001

Figure 67 (Table 5, Appendix 4) IPI(70)

Chi = 56.2436
df = 29
p < .01
ω = .20845

L = 79609.5
p < .001

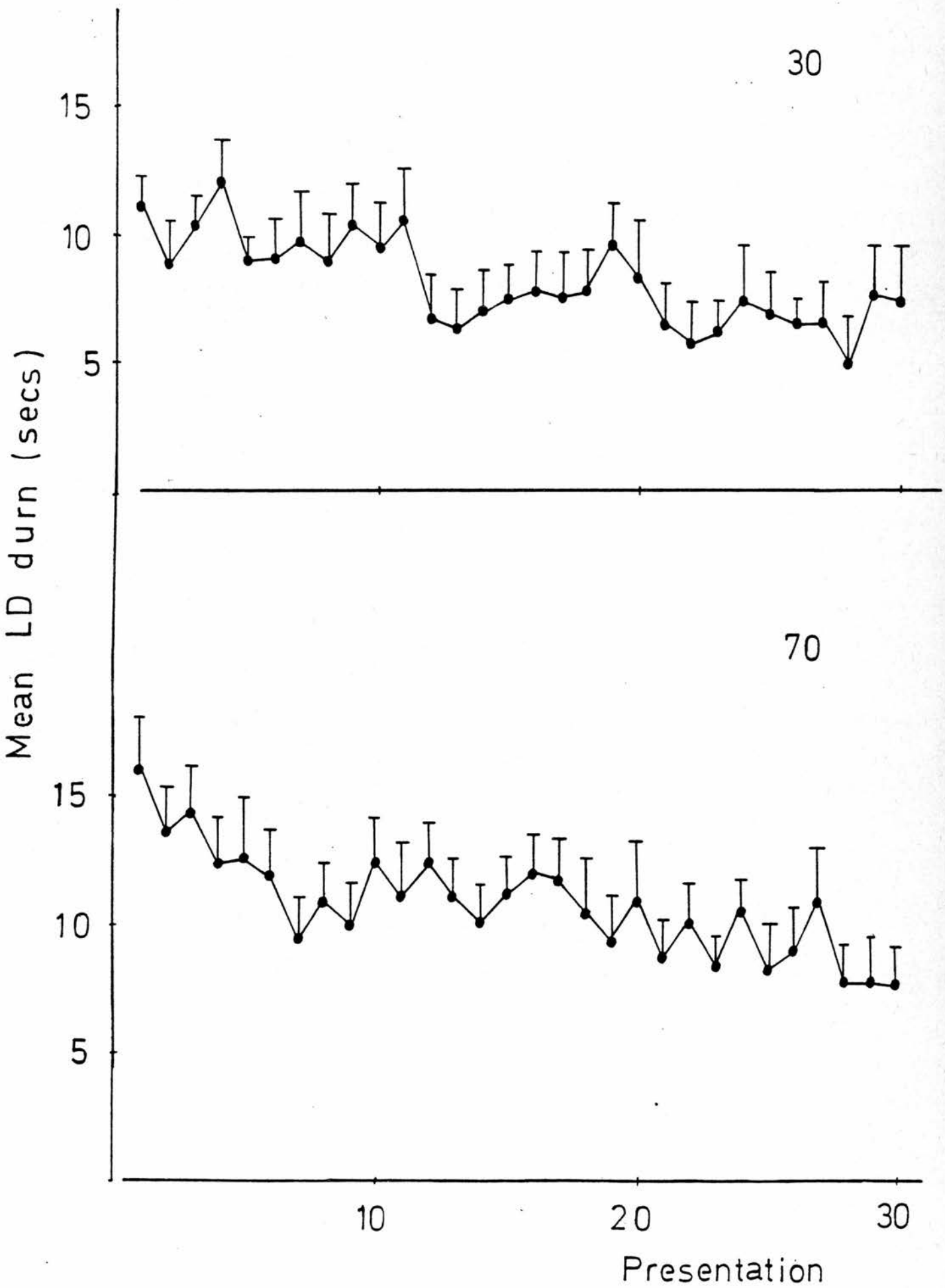
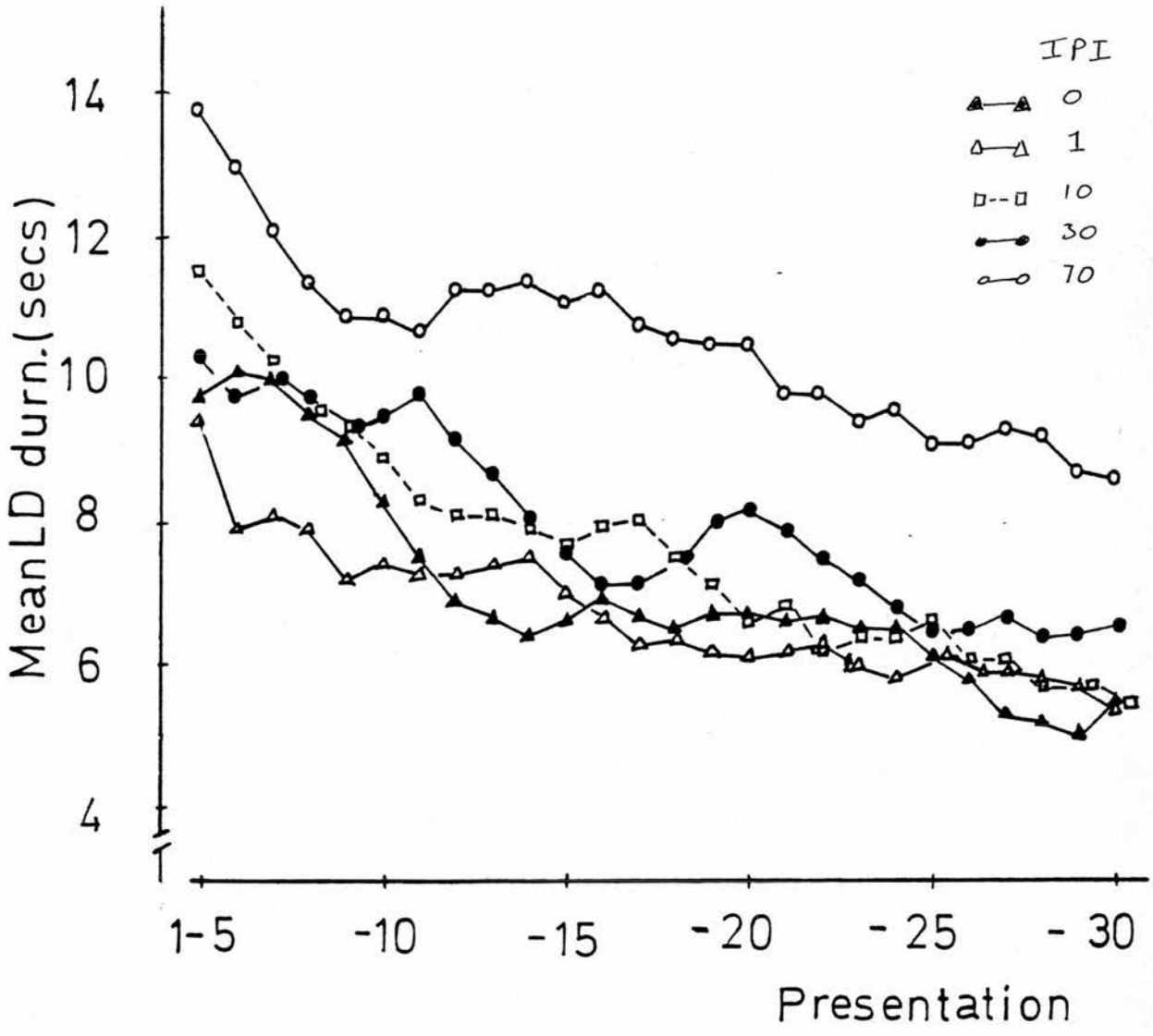

30
15
10
5
70
15
10
5
Mean LD durn (secs)
10
20
30
Presentation

Figure 68

The moving average lateral display duration (LD(d)) for successive batches of 5 presentations at each inter-presentation interval (IPI).


IPI
0
1
10
30
70
14
12
10
8
6
4
Mean LD durn. (secs)
1-5
-10
-15
-20
-25
-30
Presentation

Figures 69 - 73

Mean frequency of lateral display during successive presentations at each IPI.

Figure 69 (Table 1, Appendix 5)

IPI(0)

Chi = 26.3096
df = 29
p > .50
ω = .0913

L = 74829
p < .05

Figure 70 (Table 2, Appendix 5)

IPI(1)

Chi = 24.3257
df = 29
p > .70
ω = .0839

L = 70623.5
p > .05

Figure 71 (Table 3, Appendix 5)

IPI(10)

Chi = 42.5703
df = 29
p < .05
ω = .1467

L = 77017
p < .001

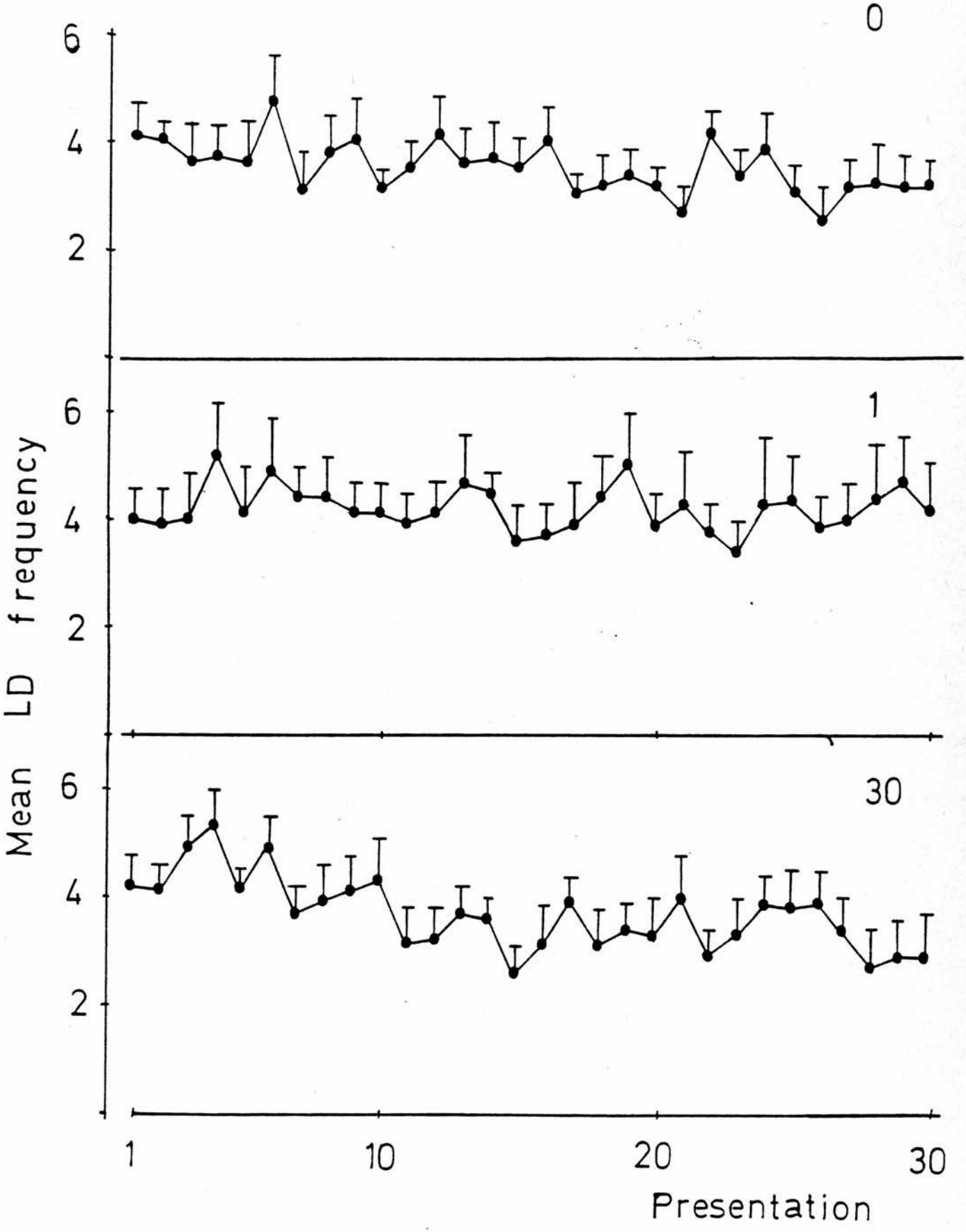

0
1
30
6
4
2
Mean LD frequency
1
10
20
30
Presentation

Figure 72 (Table 4, Appendix 5)

IPI(30)

Chi = 43.0735
df = 29
p < .05
ω = .1383

L = 75509
p < .005

Figure 73 (Table 5, Appendix 5)

IPI(70)

Chi = 26.2507
df = 29
p > .50
ω = .0904

L = 74449
p < .05

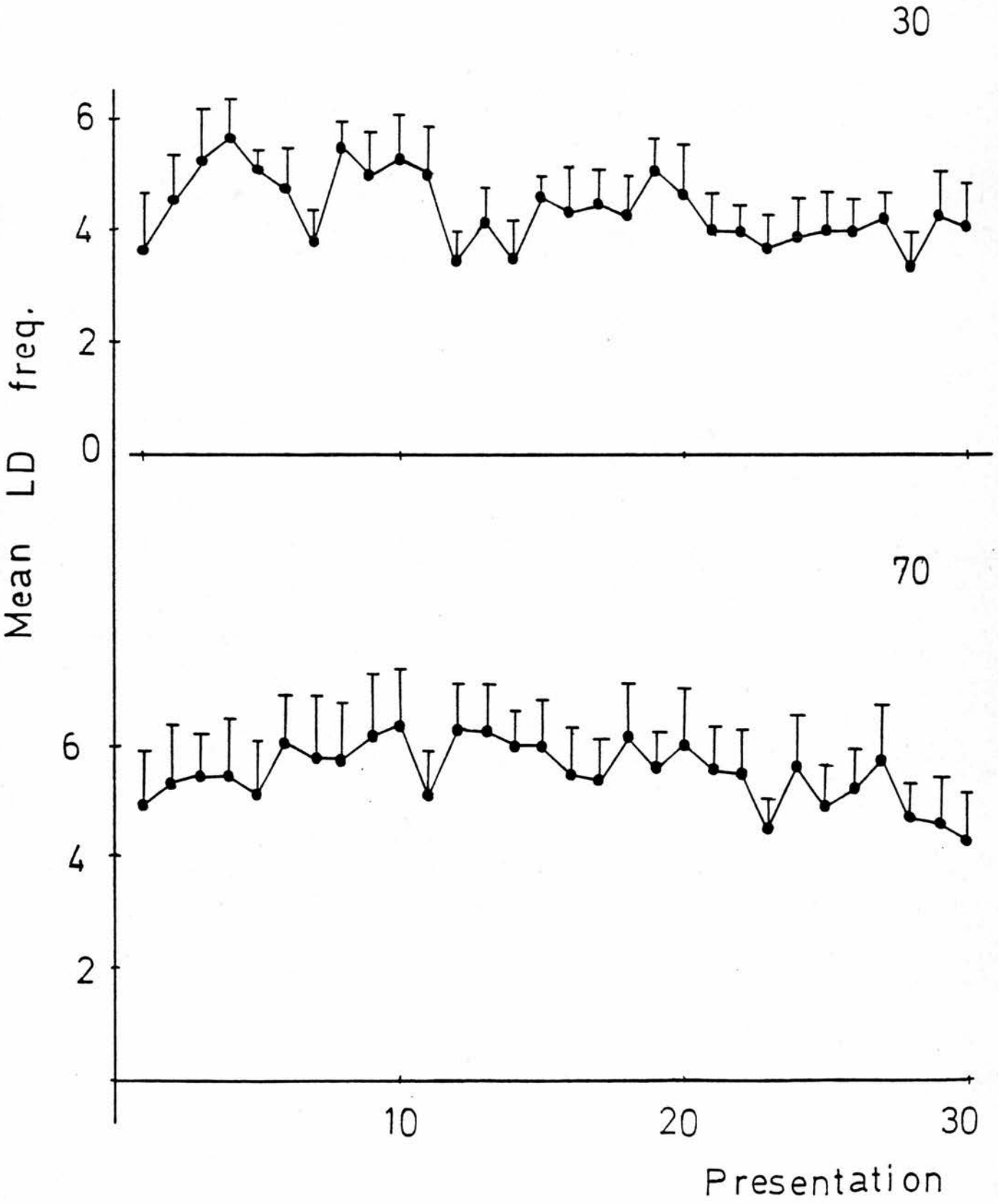
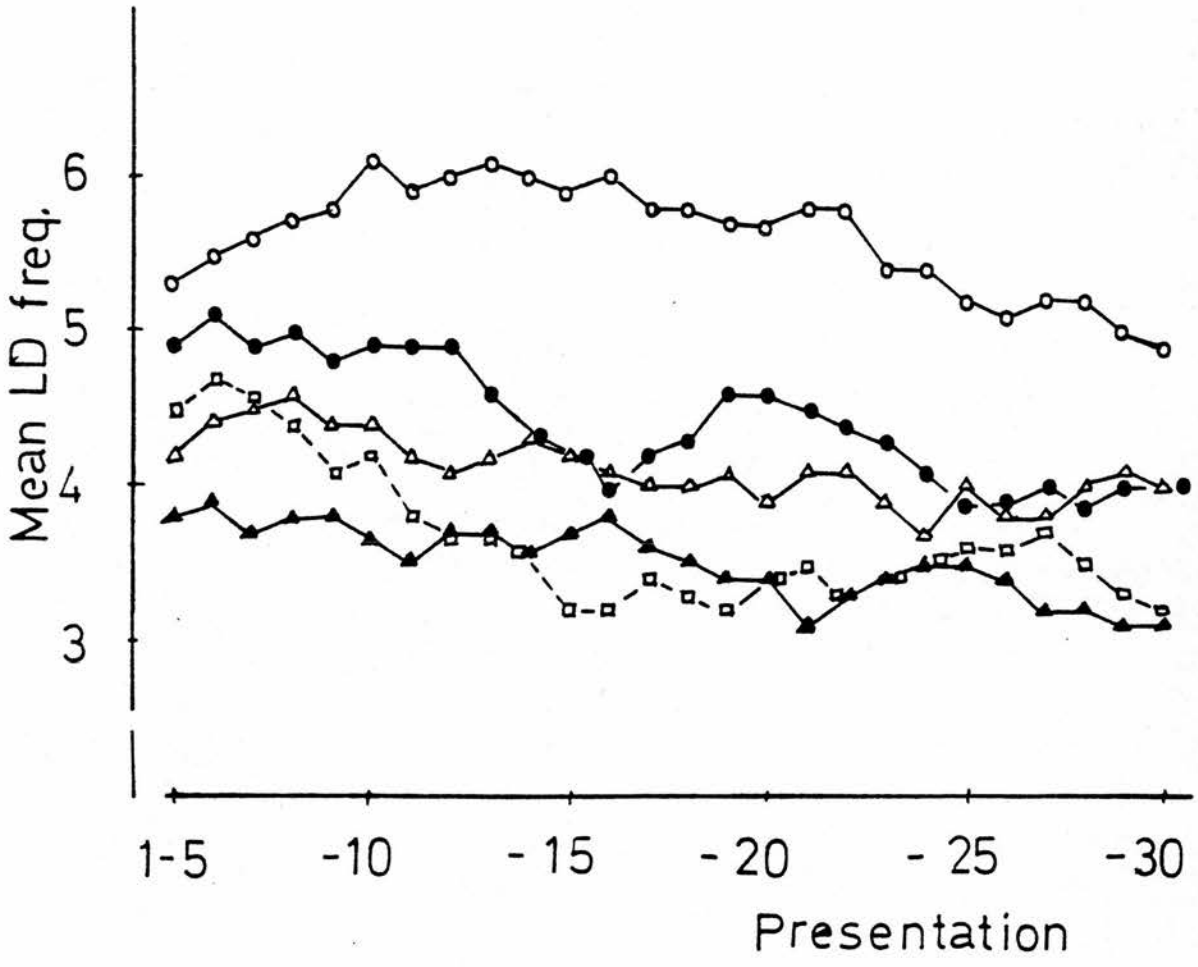

30
6
4
2
0
Mean LD freq.
70
6
4
2
10
20
30
Presentation

Figure 74

The moving average lateral display frequency (LD(f)) for successive batches of 5 presentations at each inter-presentation interval (IPI).


Mean LD freq.
6
5
4
3
1-5
-10
- 15
- 20
- 25
-30
Presentation

Figs. 75 - 79

Mean frequency of air-gulping during successive presentations at each inter-presentation interval (IPI). Bars represent one standard error. Significance testing by Friedman 2 - way analysis of variance. Spearman correlations with serial position of observation are given for each IPI. Significance levels reported for these are 1-tailed. N = 10.

Fig. 75 (Table 1, Appendix 6)

IPI(0)

Chi = 19.1321
df = 29
p > .90 $\omega = .0660$
rho with serial position = .1871
p > .05
$L = 72680$, $p > .05$

Fig. 76 (Table 2, Appendix 6)

IPI(1)

Chi = 25.9148
df = 29
p > .50 $\omega = .0891$
rho with serial position = .3298
p < .05
$L = 74781.5$, $p < .05$

Fig. 77 (Table 3, Appendix 6)

IPI(10)

Chi = 36.4360
df = 29
p > .10 $\omega = .1256$
rho with serial position = .5066
p < .01
$L = 76333.5$, $p < .005$

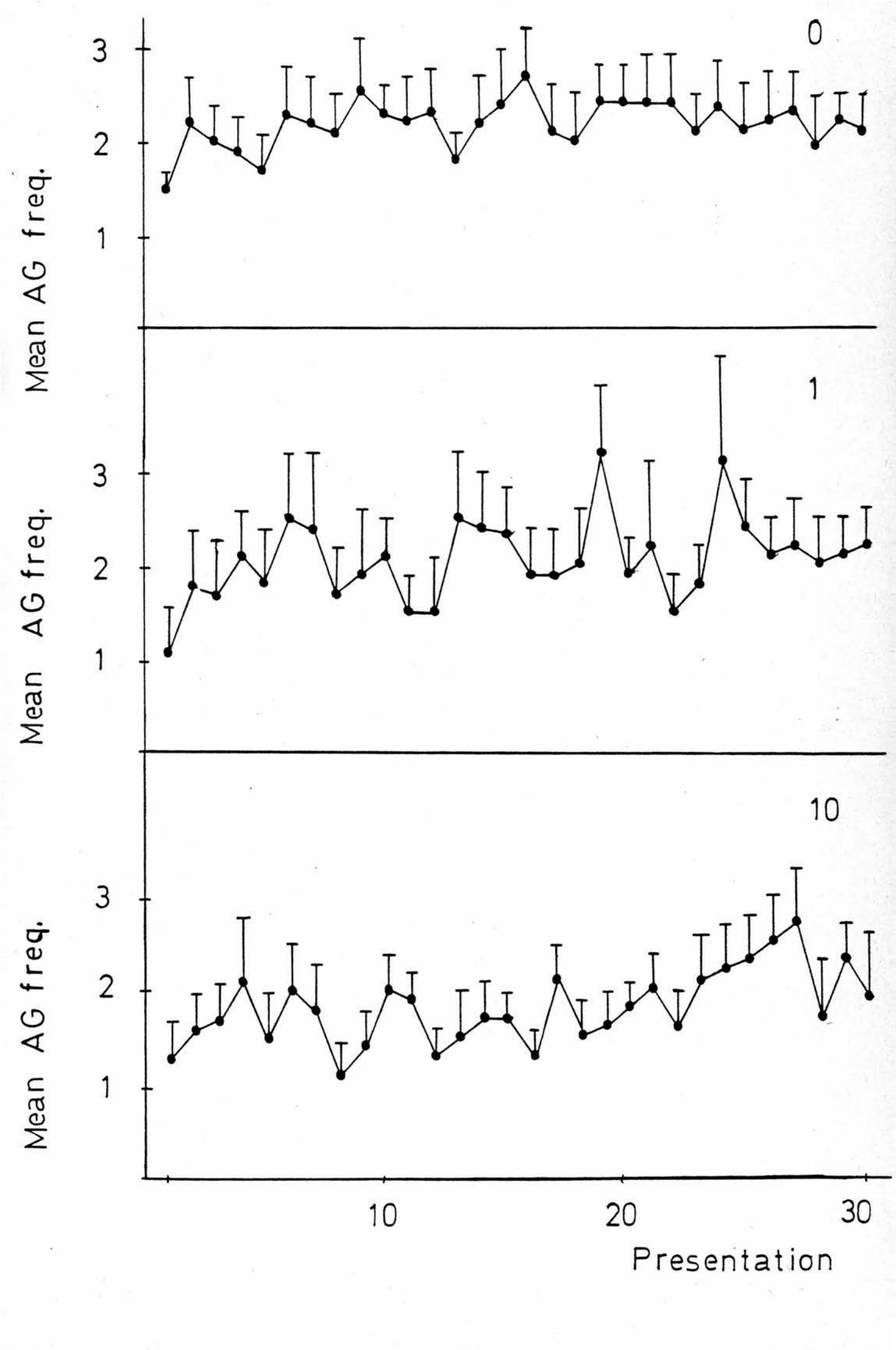

0
1
10
Mean AG freq.
Mean AG freq.
Mean AG freq.
3
2
1
10
20
30
Presentation

Fig. 78 (Table 4, Appendix 6)

IPI(30)

Chi = 25.0122
df = 29
p > .50 ω = .0865
rho with serial position = .1733
p > .05

L = 72739, p > .05

Fig. 79 (Table 5, Appendix 6)

IPI(70)

Chi = 37.8638
df = 29
p > .10 ω = .1306
rho with serial position = .4047
p < .05

L = 75149, p < .001

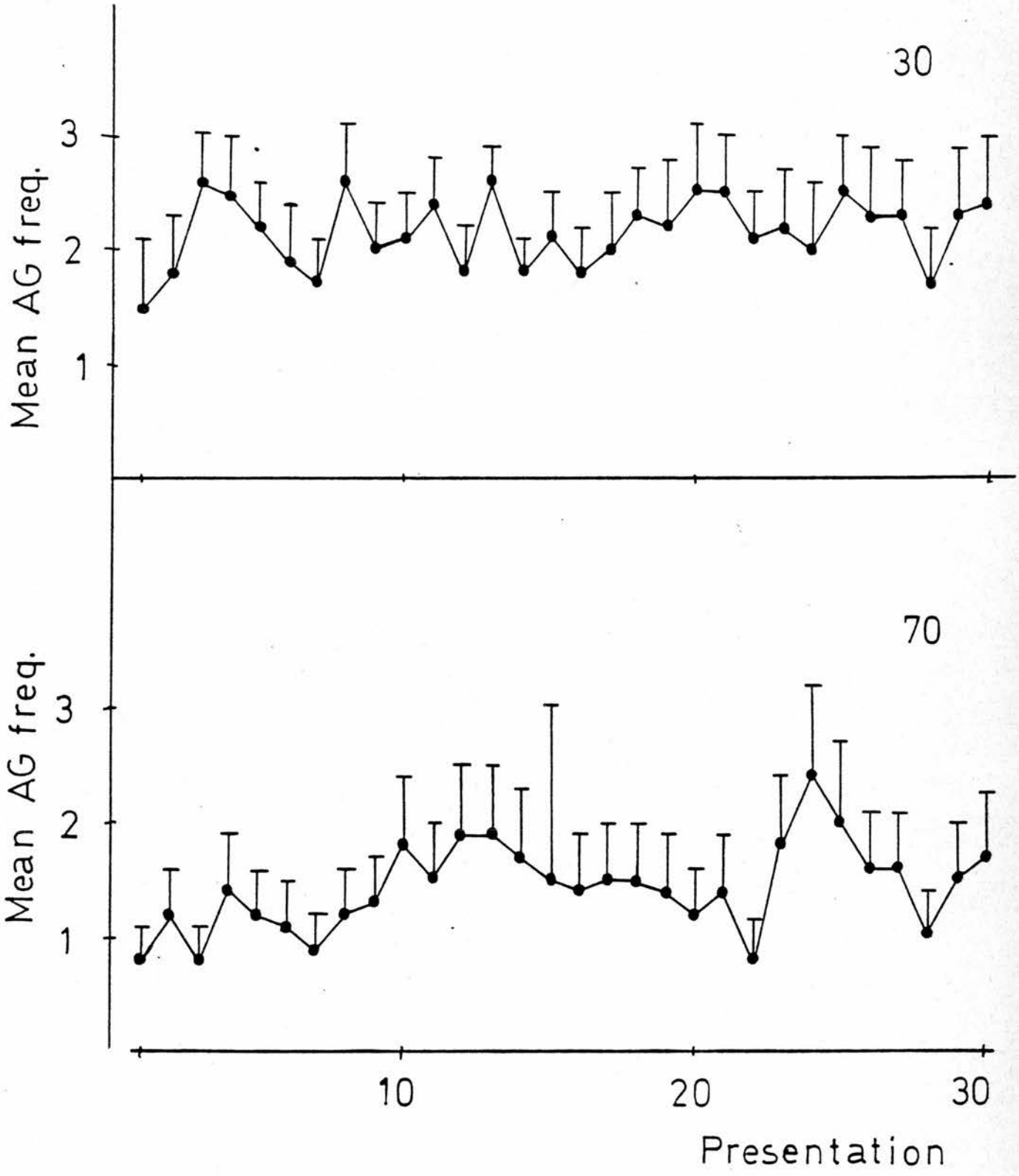

30
Mean AG freq.
3
2
1
70
Mean AG freq.
3
2
1
10
20
30
Presentation

Table 22

Pair comparisons by Wilcoxon test of biting frequency (Bi) at each inter-presentation interval (IPI). Significance levels given are 2-tailed.

IPI		1	10	30	70
0	T	5.5	22	9	2
	N	9	10	10	9
	P	$<.05$	$>.05$	$>.05$	$<.01$
1	T		9	0	1
	N		10	10	10
	P		$>.05$	$<.01$	$<.01$
10	T			14	0
	N			10	8
	P			$>.05$	$<.01$
30	T				7
	N				8
	P				$>.05$

Table 23

Mean butting frequency (Bu(f)) per presentation, paired comparisons of IPI's by Wilcoxon's test.

Significance testing was 2-tailed.

IPI		1	10	30	70
	T	11	16	11	1
0	N	9	9	10	10
	P	>.05	>.05	>.05	>.01
	T		11	11	0
1	N		10	10	10
	P		>.05	>.05	>.05
	T			20	2
10	N			10	7
	P			>.05	>.05
	T				14
30	N				9
	P				>.05

Table 24

Pair comparisons of butting duration (Bu(d)) at each inter-presentation interval (IPI). Significance levels given are 2 - tailed.

IPI		1	10	30	70
	T	27	13	10	3
0	N	10	10	9	9
	P	>.05	>.05	>.05	<.02
	T		20	10	4
1	N		9	10	10
	P		>.05	>.05	>.02
	T			20	9
10	N			10	10
	P			>.05	>.05
	T				12
30	N				10
	P				>.05

Table 25

Pair comparisons of butting mean bout length (Bu(b)) at each inter-presentation interval (IPI). Significance levels given are 2 - tailed.

IPI		1	10	30	70
	T	16.5	11.5	5.5	3
0	N	9	10	10	10
	P	>.05	>.05	<.05	<.01
	T		15	9	0
1	N		10	10	10
	P		>.05	>.05	>.05
	T			2	2
10	N			9	9
	P			<.01	<.01
	T				12.5
30	N				9
	P				>.05

Table 26

Pair comparisons of lateral display duration (LD(d)) at each inter-presentation interval (IPI). Significance levels are 1 - tailed.

IPI		1	10	30	70
	T	18	18	15	4
0	N	9	10	10	10
	P	>.05	>.05	>.05	<.02
	T		10	17	0
1	N		8	10	10
	P		>.05	>.05	>.05
	T			20	0
10	N			10	10
	P			>.05	>.05
30	T				3
	N				10
	P				<.01

Table 27

Pair comparisons of lateral display frequency (LD(f)) at each inter-presentation interval (IPI).

IPI		1	10	30	70
	T	20	9	4	0
0	N	10	7	10	9
	P	>.05	>.05	>.02	<.01
	T		19.5	14	3
1	N		9	10	10
	P		>.05	>.05	<.01
	T			8	2
10	N			10	10
	P			<.05	<.01
	T				2.5
30	N				8
	P				<.05

Table 28

Pair comparisons of lateral display mean bout length (LD(d)) at each inter-presentation interval (IPI). Significance levels given are 2 - tailed.

IPI	0	1	10	30	70
$\bar{X}$	2.0	1.8	2.1	1.9	2.1
SEM	.4	.4	.3	.3	.3
Total Ranks	28.5	27.0	35.5	26.5	32.5

Chi = 2.400

df = 4

p > .50

ω = .0600

L = 457.5

P > .05

Table 29

Comparison of lateral display duration (LD(d)) by Friedman 2 - way analysis of variance during the first presentation at each inter-presentation interval (IPI).

IPI	0	1	10	30	70
$\bar{X}$	9.0	14.3	12.8	11.1	16.1
SEM	1.9	2.9	2.1	1.1	2.0
Total Ranks	19.5	32	31.5	28.5	38.5

Chi = 7.64

df = 4

N.S.

Table 30

Mean air-gulp frequency per presentation at each inter-presentation interval (IPI). Significance testing by Friedman 2 - way analysis of variance. N = 10.

IPI	0	1	10	30	70
$\bar{X}$	2.2	2.6	1.8	2.2	2.1
SEM	.3	.4	.3	1.0	.3
Total Ranks	29.5	35.0	26.0	31.5	28.0

Chi = 1.900

df = 4

p > .70

$\omega = .0475$

$L = 456.5$

$P > .05$

CHAPTER 11

11.1 The Priming of Aggressiveness And Operant Responding

11.1 (a) Introduction

The previous experiment showed that behaviours found earlier to be negatively related* to operant latency increased with the density of stimulus presentations in time (excepting AG(f)) while the behaviour positively related* to operant latency (LD(d)) decreased with stimulus density. This suggested that, if before an operant session for display reward, subjects were pre-exposed to the stimulus fish (priming), the levels of those behaviours which were hypothesised to motivate operant responding would increase. For the same reason priming should also decrease lateral display duration. Because the effects of stimulus presentations outlast the stimulus presentation itself, these effects should persist for a length of time sufficient for an operant session to be initiated. They would then be expected to alter for a time the behaviours elicited by reward. If these do control operant responding, then priming should change both reward-elicited and operant behaviour. It may do this directly, or by depressing response-inhibiting post-reward behaviours. The experiment to be reported compares the effects of 3 stimulus pre-exposure durations, 0, 10 and 15 mins., on operant responding. The following hypotheses were advanced.

1. The amount of Bi, Bu(f), Bu(d) and AG(f) shown during rewards will increase with increases in priming duration.
2. The amount of LD(d) shown during rewards will decrease with increases in priming duration.
3. The rates of performance of the post-reward behaviours Wls(d), Wls(f), Wi, Ap, SeS(d), SeD(d) and Op-Rf will decrease with increases in priming duration.
4. The latency to operant responses will decrease with increases in priming duration.

11.2 (a) Subjects and Apparatus

9 subjects were randomly selected from those males already conditioned to perform operant responses for display reward. Their stimulus fish remained as already assigned to them. The apparatus used in this experiment was the same as for previous operant experiments.

11.2 (b) Experimental Design

Subjects can be primed by simply extending the period of pre-treatment used to supress courtship behaviours. Instead of terminating 30 secs. after the last withdrawal of the subject from the stimulus fish, the pre-treatment continues as a period of priming. Three priming durations were used in this experiment: 0mins., 10mins. and 15mins. and these conditions are referred to as P(0), P(10) and P(15) conditions respectively.

Each subject was exposed to each priming condition once, with the order of conditions within subjects determined by a pseudo-randomized block design such that each condition occurrred in each serial position three times (3conditions, 9 subjects). Testing was daily and the 3 priming days for each subject followed 4 consecutive days of stable responding.

11.2 (c) Procedure

Stimulus pre-treatment and preliminary procedure were the same as for the preceding operant experiments. The only departure from previous procedures was the extention of subject pre-treatment as priming. Thus, the subject in its home tank was placed in the experimental chamber and pre-treated by exposure to the stimulus fish; after it had shown no withdrawals for a period of 30secs., a timer was started and stimulus exposure continued for the duration assigned to that subject for that test (0, 10 or 15 mins.). After priming, the test procedure was as before, test chamber

illumination being 60secs after the end of priming and the session being initiated by the first response of the subject. Behaviour during primes was recorded, but results are not presented in this analysis.

11.2 (d) Method of Analysis

Since the effect of priming may be short lived, one basis for analysis will be the mean inter-response interval (IRI) for the first 3 responses emitted by each subject after the response that initiates the session, and the 3 rewards that precede those 3 responses. In all, only the first 15 responses (discounting the first of the session) and the first 15 rewards will be subject to analysis in this experiment. Inter-response intervals in this analysis are exclusive of reward time. If a significant difference between priming conditions is found in the mean IRI's for the first 3 rewards, then a priming effect on operant responding will be considered to have been demonstrated. To determine whether this difference lasts throughout the session, or as expected, disappears as the non-primed subjects increase their rate of responding into the session and the effects of priming decay during inter-reward intervals, the mean for the last 3 responses of the 15 considered will be compared in the 3 priming conditions.

In addition to direct comparison of the means of first and last 3 IRI's in the different priming conditions, an attempt will be made to indirectly compare the course of responding over sessions. For each condition the median IRI's over subjects for the 15 IRI's considered will be correlated (Pearson's r, Guilford, 1973) with the serial position of each IRI. Also, a straight line will be fitted to the data in each condition to describe the course of median IRI (method of least squares). It is expected that in the non-primed condition, median IRI will decline (negative correlation with serial position) while in primed conditions no

negative correlation will be found, because IRI's will have been brought down to their minimum level at the beginning of the session. If anything, primed subjects would be expected to increase their median IRI as the effect of priming decays.

The hypotheses advanced are directional, therefore significance testing will be 1 - tailed. All hypotheses were advanced before analysis and a summary of these may be given as follows:

1. Mean inter-response intervals for the first 3 intervals of the unprimed condition (P(0)) will be significantly ~~lower~~ higher than for the primed conditions (P(10) and P(15).
2. Mean inter-response intervals for the last 3 intervals of the unprimed condition (group P(0)) will be higher than those for priming conditions (groups P(10) and P(15)).
3. A negative correlations will be found between median inter-response interval and its serial position in condition P(0).
4. A positive correlation will be found between median inter-response interval and its serial position in conditions P(10) and P(15).

11.3 The Effects of Priming on Operant Responding

11.3 (a) Differences in Mean IRI's - Results

One subject died after its first priming session due to a heater-thermostat failure. The number of subjects whose data was used in analysis was therefore 8. Observational data for 3 subjects in condition P(15) and one of these subjects in condition P(10) was lost due to a computer paper-tape punch fault. For this reason the IRI data for these 3 individual subjects was taken from the Sodeco printing-counter records. To allow comparison across groups,

inter-response data for the same 3 subjects in the other conditions was also taken from their Sodeco print-outs and not from the WRATS records. Because the loss of observational data from subjects in the P(15) condition, comparison of reward elicited behaviour over the 3 conditions was not possible. For this reason, IRI's in conditions P(0) and P(10) will be compared separately from those in P(15) so that any difference between P(0) and P(10) conditions can subsequently be related to differences in reward-elicited display and post-reward behaviours. Significance testing of the differences between pairs of conditions was by Wilcoxon test.

Fig. 80 shows the results of comparisons of mean IRI's for the first 3 and last 3 intervals in conditions P(0), P(10) and P(15). The means for the first IRI's in condition P(0) did not differ significantly from those in P(10), (Wilcoxon , $p>.05$), although 5 subjects showed a lower mean IRI in the P(10) condition. The difference between P(0) and P(15) conditions for the first 3 IRI's was significant (Wilcx., $p<.025$) with 7 subjects showing a lower mean IRI than in the P(15) condition. The difference between P(10) and P(15) conditions was not significant. No significant differences were found between the mean IRI for the last 3 IRI's of P(0) sessions and those of P(10) or P(15) sessions (Wilcx., $p>.05$, for both comparisons). In addition mean IRI's at the ends of P(10) and P(15) sessions did not differ significantly.

11.3 (b) Changes in IRI Within Sessions

Figs. 81 and 82 show the mean IRI for each of the 15 successive IRI's observed for conditions P(0) and P(10)and P(0) and P(15) respectively. In addition a straight line was fitted to the data in each condition by the method of least squares, and median IRI was correlated with its serial position in each condition (Figs. 83-85). It can be seen from these

that in the P(0) condition, both mean and median IRI's decreased into the session. The correlation between median IRI and its serial position in the P(0) condition was significant (Pearson's r = .872, $p<.01$). In P(10) and P(15) conditions, however, no decline in mean or median IRI's was evident. The correlation between median IRI and its serial position in each of these conditions was not significant (Pearson's r = .111 and .148 respectively, $p>.05$). In P(10) and P(15) conditions mean and median IRI's, instead of declining, remain at low and constant levels throughout the sessions.

11.3 (c) Discussion

At the beginnings of operant sessions, both 10 and 15min. priming procedures resulted in a lower mean IRI than when no priming had been carried out. This effect was significant only for the P(15) condition. No difference in mean IRI at the end of sessions was found for any condition. Inspection of the course of median IRI's within sessions in each condition (Figs. 81 and 82) reveals that the effect of priming was to depress inter-response intervals at the beginnings of sessions at which level they remained for the rest of the session. When no priming was given, mean and median IRI's declined, the median IRI being significantly correlated with the serial position of the observation. This suggests that the effect of priming is to induce motivational states in subjects which occur naturally, but more slowly, when priming is not given. That the effect of priming in operant responding does not "wear off" as the session proceeds, may indicate that by depressing inter-response intervals priming allows rewards to come sufficiently close together (see previous experiment) to maintain much of the motivating effect that priming has produced.

One difficulty with this interpretation of the absence of a decay in priming effects, is that even at the ends of sessions when IRI's (and hence inter-presentation intervals)

are low, they are still of a duration sufficiently great to allow considerable decay of priming induced excitation (i.e. approx. 35secs.). With such an interval the full effects of priming may not be sustained throughout the session, but low inter-response intervals continue to occur. A possible explanation for this may be that there is a maximum rate of responding which can be produced by a fish, such that over this maximum, priming has little effect. Thus, even though a priming effect may decay into sessions, it does not decay sufficiently for responding to fall below its maximum rate. That this maximum rate is not simply a matter of how long it takes fish to traverse the reward-operandum distance is suggested by its duration, and the occurrence of response-inhibiting post-reward behaviours. The above discussion, and the observation that the variance in IRI decreases into unprimed sessions, while it remains low for primed sessions (Figs. 81 and 82), suggests that the susceptibility of subjects to priming is dependant on their unprimed response rate. That is, subjects which show very low IRI's at the beginnings of sessions in the unprimed condition will not much reduce their IRI's as the result of repeated reward (natural priming) in that condition. Subjects who show high IRI's at the beginnings of sessions will show a greater priming effect due to reward. It can also be hypothesised that the effect of priming procedures is greatest for subjects with the highest initial IRI's. The following analysis was performed to test these hypotheses.

11.4 The Relations Between the Initial Level of Responding and the Effect of Priming

11.4 (a) Method of Analysis

To investigate "natural priming", the mean of the first 5 IRI's and last 5 IRI's were taken in the unprimed condition. The mean IRI for the first 5 IRI's (F5) and the last 5 IRI's (L5) was computed for each subject. The difference between

these was calculated (F5-L5) and termed dP, the difference due to priming. The correlation between F5 and dP was then computed (Spearman's rho). This gives the relation between the absolute effect of "natural" priming and the level of "unprimed" responding.

The relative effect of priming was also investigated by calculating F5 and the proportionate change in responding due to priming, calculated by dividing F5 by L5. This is termed pP, the proportionate change due to priming. When pP is greater than 1, priming has decreased mean IRI. Spearman's rho was used to correlate F5 with pP.

To determine the relation between responding in the unprimed condition (P(0)), and the change in responding brought about by experimental priming (conditions P(10) and P(15)), the mean of the first 5 IRI's was calculated in each condition. These were termed F5(0), F5(10) and F5(15) according to whether they referred to the no priming condition (P(0)) or 10 or 15minute priming conditions (P(10) and P(15)). The absolute effect of priming was calculated by determining the difference between mean IRI for the first 5 IRI's of P(0) and mean IRI for the first 5 IRI's of the P(10) condition (F5 (0) - F5 (10)). This difference, referred to as dP as in the preceding analysis, is here termed dP(10) and is correlated with F5(0) (Spearman's rho) over subjects. The same procedure was followed for P(0) and P(15) differences (F5(0) correlated with dP (15)).

As in the analysis of "natural" priming, the relation between the proportional change in IRI and its initial level was determined. This was achieved by correlating (Spearman's rho) F5(0) with F5(0)/F5(10)i.e.(pP(10)). This procedure was repeated for the P(15) condition by correlating F5(0) with F5(0)/F5 (15) (i.e. F5(0) and pP(15)).

Because it was hypothesised that the effect of priming will be positively related to mean IRI's before priming, all significance testing of correlations was 1 - tailed.

11.4 (b) Results

For fish in the non priming condition (P0), Table 31(a) shows the correlation between the mean of the first 5 IRI's occuring during the session and dP(0) (difference due to priming at the end of the session). Spearman's rho was .952 ($p<.01$). Table 31(b) shows the correlation between the initial level of responding (F5(0)) and the proportionate change due to priming (pP(0)). Spearman's rho was significant at .810 ($p<.05$).

The relations between initial mean IRI in the unprimed condition and the absolute change in initial IRI produced by the P(10) condition (dP(10)) is represented in Table 31(c). The correlation between F5(0) and dP(10) is .881 (Spearman's, $p<.01$). Table 31(d) shows the correlations between initial mean IRI in the P(0) condition and the proportionate change at the beginning of the P(10) condition (pP(10)) is .857 (Spear., $p<.01$).

For the P(15) condition, the correlation between F5(0) and the absolute change due to 15min. priming (dP(15)) is .643 (Spear., $p<.05$). (Table 31(e)). Table 31(f) shows the correlation between the proportionate change in mean IRI due to 15mins. of priming pP(15), and F5(0). Spearman's rho = .643 (Spear., $p<.05$).

11.4 (c) Discussion

Concerning the "natural" priming which occurs in the P(0) condition as a consequence of repeated reward, both the absolute and relative amounts of facilitation in operant responding which occur during the session were correlated positively with the initial mean inter-response interval. Thus, subjects which begin the session with high IRI's decrease their IRI's into the session more than subjects which start the session with low IRI's. The amount of "natural" priming in terms of response rate, which occurs in a session may therefore be limited by an upper ceiling on response rate.

A similar ceiling may operate in restricting the effect of priming by pre-exposure to the reward stimulus. The absolute and relative amounts by which priming lowers inter-response intervals (increases response rate) were positively correlated with the mean inter-response interval at the beginnings of sessions in which priming was not administered. Thus, priming procedures were most efficacious with subjects which responded at a low rate without priming. Since the lowest mean IRI over the first 5 IRI's of the first 5 IRI's of the P(0), P(10) and P(15) conditions was 19.9, 17.8 and 17.1 secs. respectively, this ceiling is not likely to be a result of insufficient time being available to swim from reward to response gate. It is more likely that post-reward behaviours, of which some amount always occurred, cannot be inhibited below some finite level. It can be suggested that this level may constitute an important source of individual differences.

11.5 Changes in Reward-Elicited & Post-Reward Behaviours Due to Priming

15mins. pre-exposure of subjects to the display eliciting stimulus significantly decreased their mean inter-response intervals at the beginnings of operant sessions with that stimulus as reward. With 10mins. pre-exposure, the effect of priming on mean IRI's was not significant, but the pattern of median inter-response intervals during sessions was altered such that they did not decrease significantly as they do in sessions without priming. This effect was also found with 15mins. priming. This priming effect on operant responding may be related to priming induced changes in post reward behaviours and/or reward elicited display. The following analysis will attempt to describe these changes quantitatively and relate them to the changes in operant behaviour already shown to have occurred.

Because of the loss of observational data for 3 subjects

in the P(15) condition, no attempt will be made here to analyse priming induced changes in non-operant behaviour in that condition. Although the effect of 10mins. priming on operant behaviour is a much less certain effect, since it has only been shown that the pattern of median IRI's over sessions is altered, the P(10) condition will be analyzed for priming-induced changes in post-reward and reward-elicited behaviours. The possibility of statistical treatment of the results which is afforded by a full complement of subjects in the P(10) condition will at least allow the formulation of tentative hypotheses about the relations between these behaviours and operant performance.

Since some priming effect has been demonstrated and since the experiments reported in chs. 8.4 and 9.2, implicated only some post-reward and reward-elicited behaviours in the control of operant responding, only those will be analyzed here. It was hypothesised that priming by pre-exposure to a display eliciting stimulus decreases inter-response intervals in the operant situation by:

1. Decreasing the rate of performing of the operant response inhibiting post-reward behaviours Wls(d), SeS(d), SeD(d), Wls(f), Ap, Wi and Op-Rf.
2. Decreasing the amount of the operant response-"inhibiting" reward-elicited behaviour LD(d).
3. Increasing the amounts of the operant response "facilitating" behaviours Bi, Bu(f), Bu(d) and AG(f).

11.5 (a) Post-Reward Behaviours - Methods of Analysis

To discover whether priming decreased the rates of performance of post-reward behaviours, the total amount of each behaviour was calculated for the first 3 post-reward intervals observed. This mean was then expressed as a rate by dividing it by the mean duration of those 3 intervals (operant latencies), as derived from WRATS records. A similar means of expressing amounts of post reward behaviours

as rates was used for the last 3 post reward intervals of the 15 observed. A priming effect of depressing the rates of performance of post-reward behaviours was considered demonstrated if the mean rate of a behaviour for the first 3 post-reward intervals was significantly greater in the P(0) condition than in the P(10) condition (Wilcoxon test, 1 - tailed). In addition, to determine the degree to which any effect found persists into the session, a similar comparison of mean rates was carried out for the last 3 post reward intervals observed. It was expected that the P(10) condition would produce the lowest rates. To determine whether priming produced a change in the pattern of mean rate of post-reward behaviour, a comparison of the mean rate at the beginnings of sessions (first 3 intervals) and at the ends of sessions (last 3 intervals) was made for both P(0) and P(10) conditions. It was hypothesised that since mean inter-response interval declines in the P(0) condition, that where any difference is found between the beginnings (F3) and ends (L3) of sessions in either condition, higher rates of performance of the behaviour would be found at the start of sessions.

11.5 (b) Post-Reward Behaviours - Results

Table 32 shows the results of comparisons (Wilcoxon) of mean rates of post-reward behaviours at the beginnings (F3) of sessions in the conditions P(0) and P(10). Also shown are the results of comparisons of conditions at the ends (L3) of sessions, and the results of comparisons of F3 and L3 within conditions. For the behaviours Wls(f), Wls(d), SeS(d) and SeD(d) no significant differences between conditions were found. Differences across sessions within conditions were also found not to be significant.

For the post reward behaviours Op-Rf, Wi and Ap, the comparisons made did reveal some significant differences,

but not ones which can be immediately attributed to the effects of priming. Considering Wi and Ap, comparisons of F3 in P(0) and P(10) conditions produced differences which were not in the predicted direction, but which were significant when significance testing was 2 - tailed. The P(10)condition was found to produce significantly higher rates of both of these behaviours at the beginnings of sessions. This could be a result not of an increase in Ap and Wi, but of the decrease in operant latency produced by priming. That is, the absolute amounts of these behaviours may be similar in both conditions, and the difference found may be due to expressing these amounts as rate measures. To test this, the mean absolute amounts of Ap and Wi during the first 3 intervals were compared over conditions. Table 32 shows that the mean absolute frequencies in F3, of Ap and Wi respectively, do not differ significantly between P(0) and P(10) conditions. The effect of priming on the rates of these behaviours must therefore be attributed to the effect on operant latency.

The only significant effects remaining are the higher rates of Wi and Ap at the beginnings of P(10) sessions than at the ends of sessions in that condition. Since the operant latencies at the beginnings and ends of P(10) sessions do not differ significantly, this effect is not likely to be due to the expression of these behaviours as rates. Comparison of the mean absolute amounts at F3 and L3 in the P(10) condition for Ap and Wi reveals that significantly less Ap occurs at L3, while Wi shows no significant decline from F3 to L3 (Table 32).

11.5(c) Discussion

One significant effect of priming on the rates of post-reward behaviours was to increase Ap and Wi. However, this could be accounted for by the decrease in operant latency produced by P(10). Also found was a decrease in

the rates of Ap and Wi over P(10) sessions. Since P(0) and P(10) conditions did not differ in mean inter-response intervals at the ends of sessions, the decrease in Ap and Wi which occurred over P(10) sessions can have had little effect of decreasing operant latency. How these changes in Ap and Wi might be related to changes in reward elicited behaviour during P(10) sessions will be considered later.

11.5 (d) Reward Elicited Behaviours - Methods of Analysis

To investigate the changes in reward-elicited behaviours due to priming, methods of analysis were used similar to those used for post-reward behaviours. As before, only the first 15 rewards of sessions were considered. The mean amounts of behaviours for the first 3 and last 3 rewards were calculated (F3 and L3 respectively) in each condition (P(0) and P(10)). A change in behaviour due to priming will be considered to have been demonstrated if the mean amount of behaviour at the beginnings of sessions (F3) or at the ends of sessions (L3) differs significantly in P(0) and P(10) conditions (Wilcoxon test). Changes in behaviour over sessions in each condition were examined by comparing the amounts occurring at the beginnings (F3) and at the ends (L3) of sessions in the P(0) and P(10) conditions.

It was hypothesised that the reward-elicited behaviour "inhibitory" with respect to operant responding (LD(d)) would be depressed by priming at the beginnings and ends of sessions. Mean LD(d) at F3 and L3 should therefore be greater in the P(0) condition. It was hypothesised that behaviours "facilitatory" with respect to operant responding (Bi, Bu(f), Bu(d) and AG(f)) would be greater at the beginnings and ends of P(10) sessions, than in P(0) sessions. It was also hypothesised that where changes over sessions occurred in either condition, they would involve a decline in LD(d) and increase in Bi, Bu(f), Bu(d) and AG(f). Because of the

directional nature of these hypotheses, all significance testing was 1 - tailed.

11.5 (e) Results

The course of Bi over P(0) and P(10) session is shown in Table 33 , and Fig. 86 shows the course of Bu(d) and Table 34 the course of Bu(f). It was expected that these attack behaviours would be produced at the beginnings of sessions by priming. Instead, few attacks occurred at the start of sessions in either condition. Into P(10) sessions, attacks increased, while no such increase occurred in the P(0) condition. No statistical analysis of attacks was carried out because only 1 unprimed subject and 5 in the primed condition showed any attack behaviours at all.

The course of AG(f) in both conditions can be seen in Fig. 87. It can be seen that AG(f) increased in the P(0) condition but remained at a high level throughout P(10) sessions, Spearman's rho between mean AG(f) and serial position in P(0) and P(10) conditions are .7990 ($p<.01$) and .4933 ($p<.05$) respectively (1 - tailed). Table 35 shows that at the beginnings of sessions (F3), P(10) produced significantly higher AG(f) than P(0). At the ends of sessions (L3), no significant difference between conditions remained. In the P(0) condition AG(f) was significantly lower at F3 than at L3 but no significant change over sessions occurs in the P(10) condition.

Fig. 88 shows the course of LD(d) over sessions in P(0) conditions. P(0) subjects showed a slight decline in LD(d) over the session, while P(10) subjects began at a lower level and remained at that level. Table 35 shows that a priming effect on LD(d) did occur. At the beginnings of sessions, the P(10) condition produced significantly less LD(d) than the P(0) condition, but the difference between conditions at the ends of sessions was not significant. LD(d) at the beginnings of the P(0) condition was significantly higher

than at the end, while no significant change over P(10) sessions occurred.

11.5 (f) Discussion

Priming by 10mins. pre-exposure to the reward stimulus changes the behaviour elicited by subsequent rewards. The display LD(d), which is positively related* to operant latency, was significantly depressed during the first 3 rewards after priming. This effect did not persist until the last 3 rewards of the 15 considered, because the unprimed condition still involves its own "natural" priming processes which reduced the level of LD(d) to that produced by experimental priming. Similar effects of priming on AG(f) were found, but this behaviour was increased by priming. As for LD(d), the effect of priming on AG(f) did not persist until the last 3 rewards of the session, because subjects in the unprimed condition increased their AG(f) over successive rewards.

The effect of priming on attack behaviours differs from its effects on LD(d) and AG(f). Instead of producing a difference in behaviour between primed and umprimed conditions which then disappears because of "natural" priming, overt attack did not occur until the ends of sessions preceded by 10mins. of priming. Little attack occurred when no priming had been administered. In the primed condition, therefore, priming must produce an increase in the attack tendency of subjects, which is insufficient to immediately produce attacks during reward. However, when this increased tendency is further incremented by the cumulative effects of rewards, overt attacks then occur.

11.6 Reward-Elicited Behaviours, Post-Reward Behaviours and the Control of Operant Responding

It was shown that 15mins. priming significantly increased

operant response rate for a short time afterwards. A nonsignificant effect, but in the same direction, was produced by 10mins. of priming. Both priming durations used changed the pattern of median inter-response interval over the session. The question being asked is, what was the effect of priming on post-reward and reward-elicited behaviours such that these effects on operant responding occurred.

The effects of priming on non-operant behaviour discovered in preceding analyses are those produced by 10mins of priming. Since this condition did not produce an effect on operant responding which was statistically significant, other than that of changing the pattern of median IRI's within sessions, an attempt to relate the changes produced by priming in non-operant behaviour to its effect on operant responding, must necessarily result in only tentative conclusions.

Accompanying the priming induced reduction in inter-response intervals was a decrease in LD(d) and an increase in AG(f). Since AG(f) was earlier found to be negatively related* to operant latency and unaffected by inter-presentation intervals of up to 70sec. (lower than some occurring in this experiment) and now shown to be increased by a procedure which also reduces inter-response intervals, AG(f) must be one output of a system involved in the control of operant behaviour. It has already been suggested that AG(f) may be an indicator of a subject's level of activity and thus an indirect measure of its attack tendency.

Priming depresses LD(d), a reward-elicited behaviour earlier found to be positively related* to operant response latency. The dependence of LD(d) on the inter-reward interval revealed by Experiment 7 (ch. 10) meant that the

direction of causal relations between it and the operant latency could not previously be determined. However, by priming LD(d) was reduced, and this was accompanied by the changes in operant responding described. It must be concluded that LD(d) reflects the action of a system which is inhibitory towards operant responding, or else high LD(d) indicates a low level of the attack tendency.

Concerning overt attacks, no evidence emerged to suggest that these are necessary for an effect of priming on operant responding. Priming-induced increases in attack are not contemporaneous with effects on operant responding, and neither do inter-response intervals decrease further when overt attacks do eventually increase. This result is in agreement with the earlier observation that when operant response latencies decrease into unprimed sessions, this change occurs before overt attack is reliably elicited. Since the negative relations* between attack and operant response latency discovered in ch. 8 can be accounted for by the negative relation between attack and the inter-presentation interval, these behaviours or the motivational state underlying them cannot with any confidence be implicated directly in the motivation of operant responding. That attack behaviours do indirectly have a facilitatory effect is indicated by their negative relations* with operant response-inhibiting post-reward behaviours. The relations between reward-elicited behaviours and operant responding is not in this experiment amenable to explanation by intermediate effects of these behaviours on post-reward behaviours. No post-reward behaviours considered were suppressed at the start of sessions in the priming condition. The effect of post-reward behaviours on operant responding

as they are indicated by the measures and methods of analysis used in ch. 9.2, is most reliable for Wls(d), since the correlations found satisfied the criterion for a relation*. However, even this behaviour was not reduced significantly by the increase in attacks which occurred at the ends of P(10) sessions. The significant decrease in the post-reward behaviour Wi, which occurred only in the P(10) condition, and was not sufficient to produce a significant difference between P(0) and P(10) conditions, can however be accounted for by the increase in attack which occurred in the P(10) condition. Ch. 9.3 showed that Bi was negatively related* to Wi. The similar decrease over the P(10) condition in Ap cannot be accounted for in the same way, since a negative relation* between this behaviour and attacks was not found in that experiment.

In ch. 8.1(c), the question of whether the display elicited by a stimulus or the characteristics of the stimulus itself determined operant performance was raised. It was mentioned that a possible method of separating these factors would be suggested. In the previous experiment, a live male conspecific was used as a reward stimulus, but if instead of this, a model Betta in aggressive display were used, the model would be constant in the stimulus characteristics it presents, while the display behaviour of the subject would be altered for a time by priming with a conspecific. The effects of display on operant behaviour could then be separated from the effects of the reward stimulus itself.

The results of the priming experiments reported by Hogan and Bols (1980) have been discussed in ch. 8.1(c). They report that in the runway situation primed male Bettas showed both increased swimming speed and preference for display over food reward. They did not, however, show that the behaviour elicited in subjects during rewards was modified. The experiment reported in this chapter showed that operant response rate could be increased by priming

and described the effects of such priming on reward elicited and post reward behaviours.

Rasa (1971) has also demonstrated an effect of priming on operant behaviour for display reward. Juvenile damselfish (Microspathodon chrysurus) having learned to enter a bottle to see a conspecific antagonist, showed an increased frequency of bottle entries for 5mins. following the presentation of a model conspecific. Comparison with the results of the present experiment is difficult, however, because the effect of priming on single non-operant behaviour is reported, and this occurs between rewards, not during them. It does not, however, correspond to the response-inhibiting behaviours reported here since this behaviour (snapping) is an index of aggressiveness.

The results of the present and the previous experiment (ch. 10) taken together lead to an important conclusion about the control of operant responding for display reward. The systems underlying the reward-elicited behaviours LD(d) and AG(f) may be directly involved in controlling the operant response. LD(d) and other behaviours (Bi, Bu(f) and Bu(d)) may indirectly control operant behaviour by their effects on post reward behaviours. With the possible exception of AG(f), all these operant response-controlling behaviours are themselves determined by the inter - reinforcement interval. Since some time must always elapse between rewards while fish perform the operant response, and since the occurrence of post-reward behaviours may impose an upper ceiling on operant response rate, the response-motivating effects of reward will decay between reinforcements. Thus the characteristics of the systems controlling operant behaviour for display reward are such that they interact with a characteristic of all operant situations, that is, the existence of an inter-reinforcement interval. It follows from the above hypothesis, that anything that serves to increase

the inter-reward interval will lower operant response rate. The following chapter is concerned with two commonly used experimental manipulations which involve increasing the minimum inter-reward interval which can occur; the withholding of reward in extinction, and the imposition of a fixed ratio requirement.

Figure 80

Comparisons of the mean inter-response intervals for the first 3 and last 3 intervals occurring in each priming condition. Bars represent one standard error. Comparisons by Wilcoxon test.

first 3 IRI's (secs.)			last 3 IRI's (secs.)		
Priming (mins.)	Mean	SEM	Priming (mins.)	Mean	SEM
0 :	73.7	22.0	0 :	34.6	3.4
10 :	43.5	7.4	10 :	40.8	7.0
15 :	47.8	15.4	15 :	46.9	11.4

Prime :		0	15
10	T	10	14
	N	8	8
	P	N.S.	N.S.
15	T	3	
	N	8	
	P	$< .025$	

Prime :		0	15
10	T	13	16
	N	8	8
	P	N.S.	N.S.
15	T	12	
	N	8	
	P	N.S.	

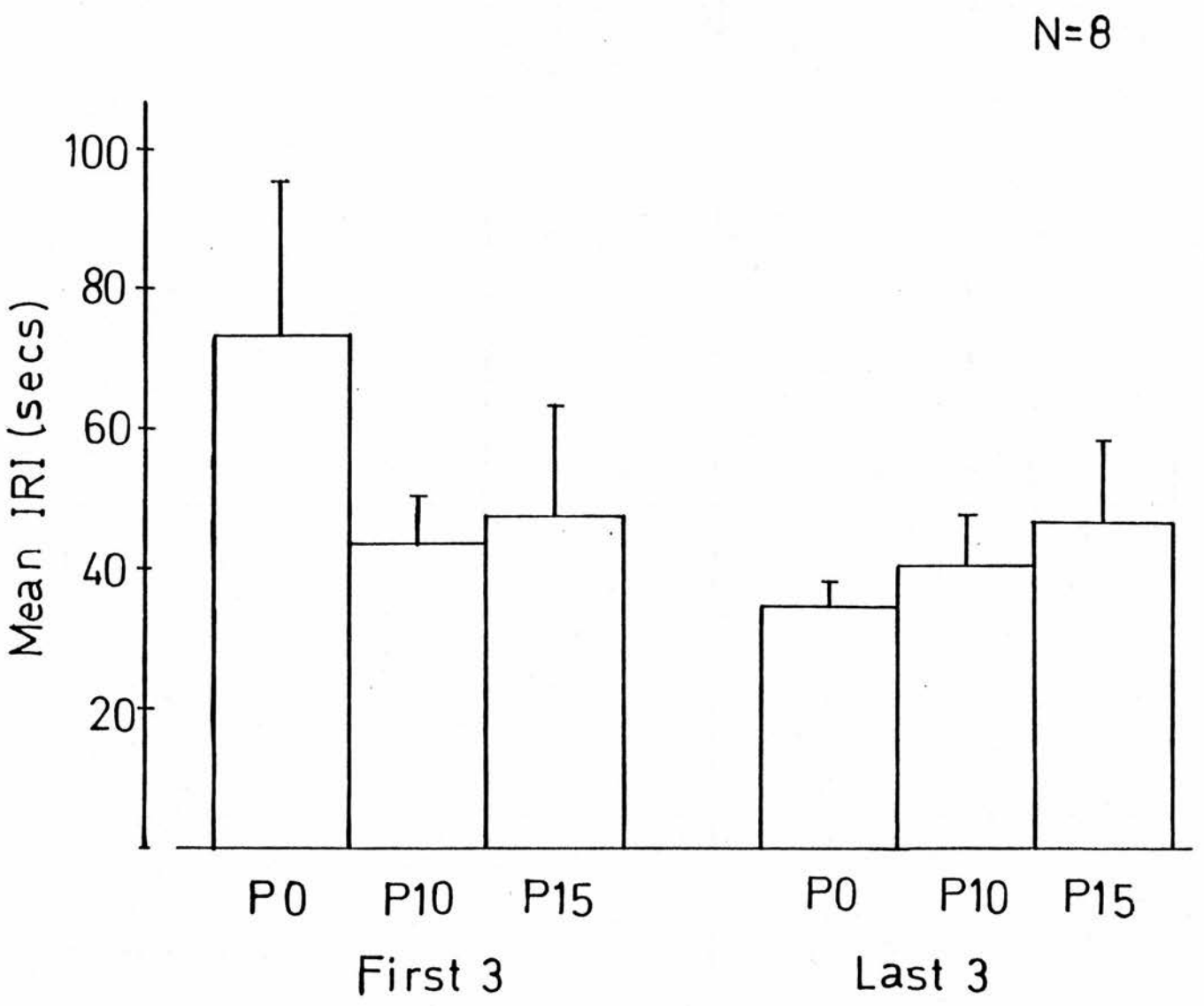

N=8
100
80
60
40
20
Mean IRI (secs)
P0
P10
P15
P0
P10
P15
First 3
Last 3

Figure 81

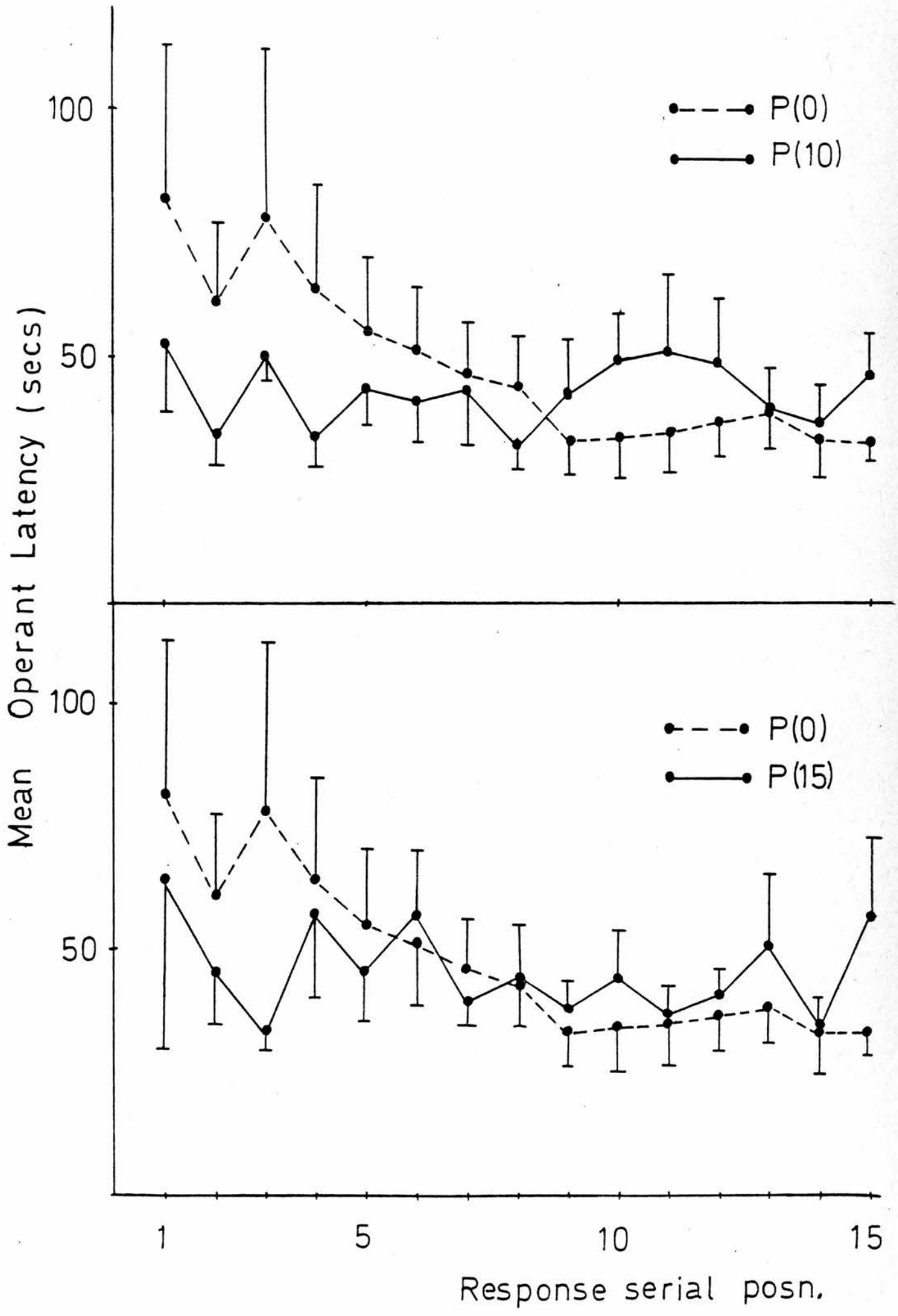
The course of mean operant latency (inter-response interval) over the first 15 responses of the session in 0 mins. priming (P(0)) and 10 mins. priming (P(10)) conditions.

Bars represent one standard error. N = 8.

Figure 82

The course of mean operant latency (inter-response interval) over the first 15 responses of the session in 0 mins. priming (P(15)) conditions.

Bars represent one standard error. N = 8.


100
50
P(0)
P(10)
100
50
P(0)
P(15)
Mean Operant Latency (secs)
1
5
10
15
Response serial posn.

Figures 83 - 85

The change in median inter-response interval (IRI) over the 15 observed in the 0, 10 and 15 min. priming conditions (P(0), P(10) and P(15)). Straight line fitted by method of least squares. Broken lines each indicate one standard error of estimate. The Pearson correlations between median IRI and the observation serial order are given below. Significance levels reported are 2 - tailed.

Priming duration (mins.)	Pearson's r
0	$r = -.873$ $p < .01$
10	$r = -.111$ $p > .05$
15	$r = -.148$ $p > .05$

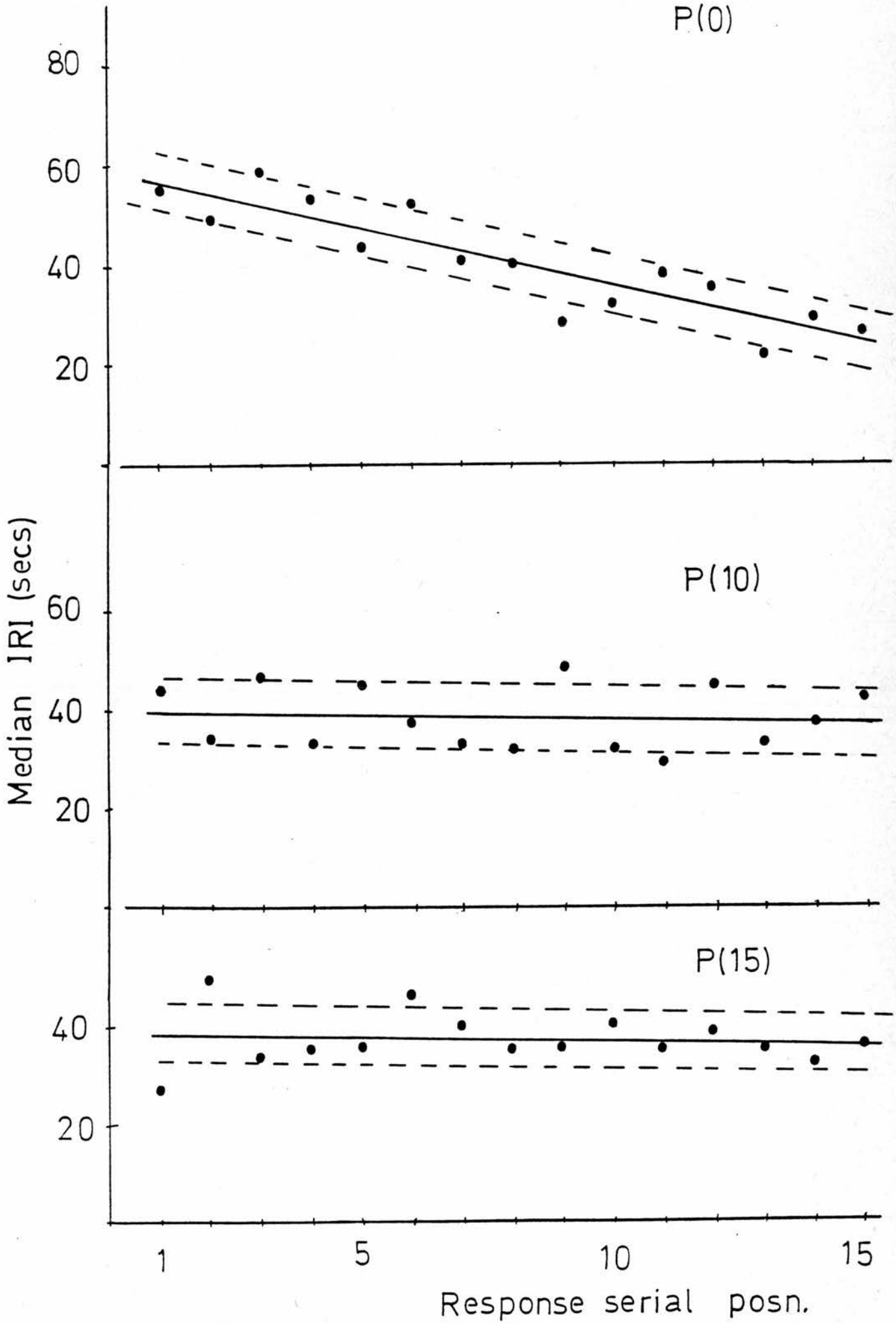

P(0)
80
60
40
20
P(10)
60
40
20
P(15)
40
20
Median IRI (secs)
1
5
10
15
Response serial posn.

Figure 86

The course of mean butting duration (Bu(d)) over successive rewards in sessions with 0 mins. priming (P(0)) and 10 mins. priming (P(10)). Bars represent one standard error. N = 8.

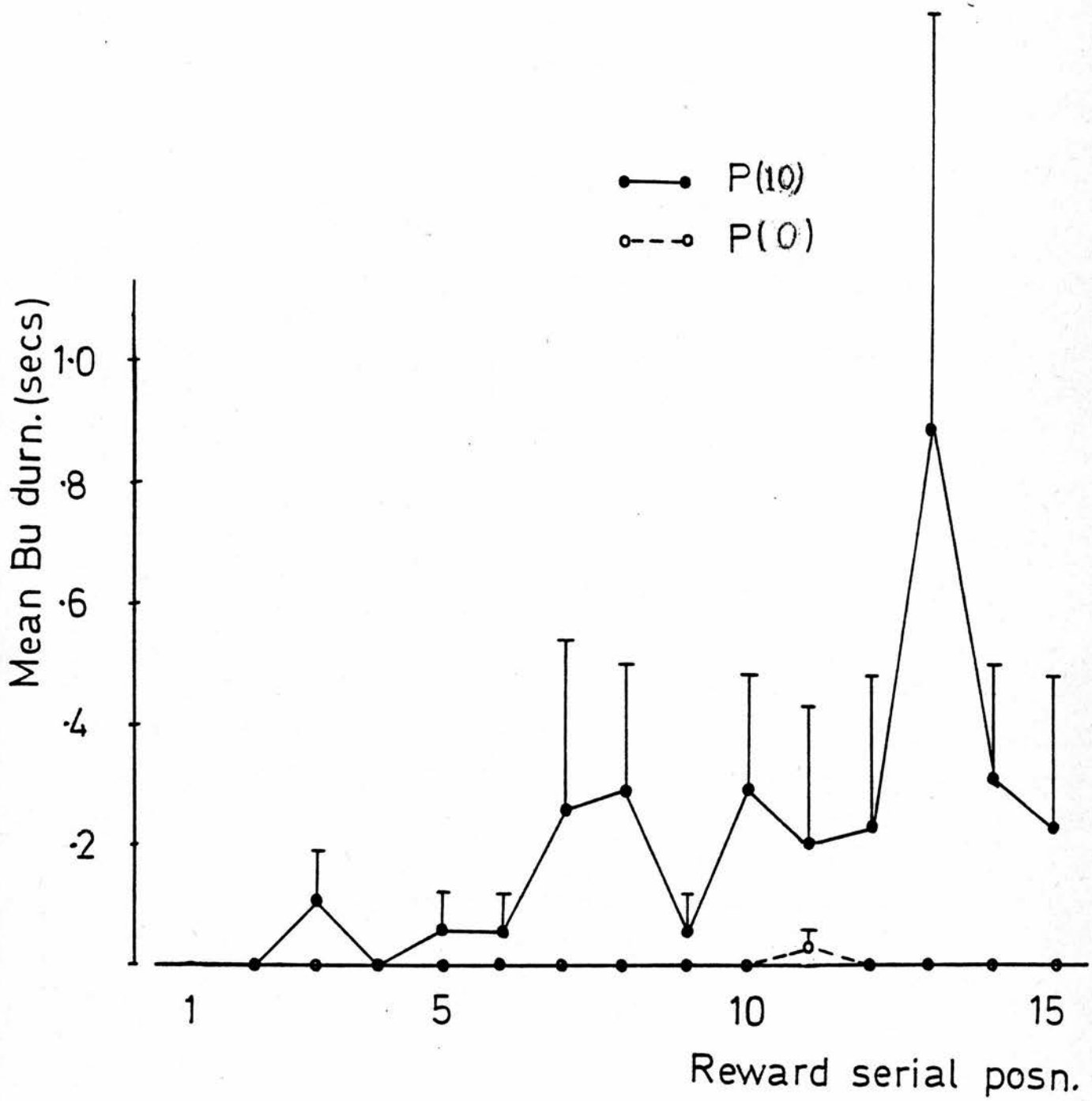

P(10)
P(0)
Mean Bu durn. (secs)
1·0
·8
·6
·4
·2
1
5
10
15
Reward serial posn.

Figure 87

The course of mean air gulp frequency (AG(f)) over successive rewards in sessions with 0 mins. priming (P(0)) and 10 mins. priming (P(10)). Bars represent one standard error. N = 8.

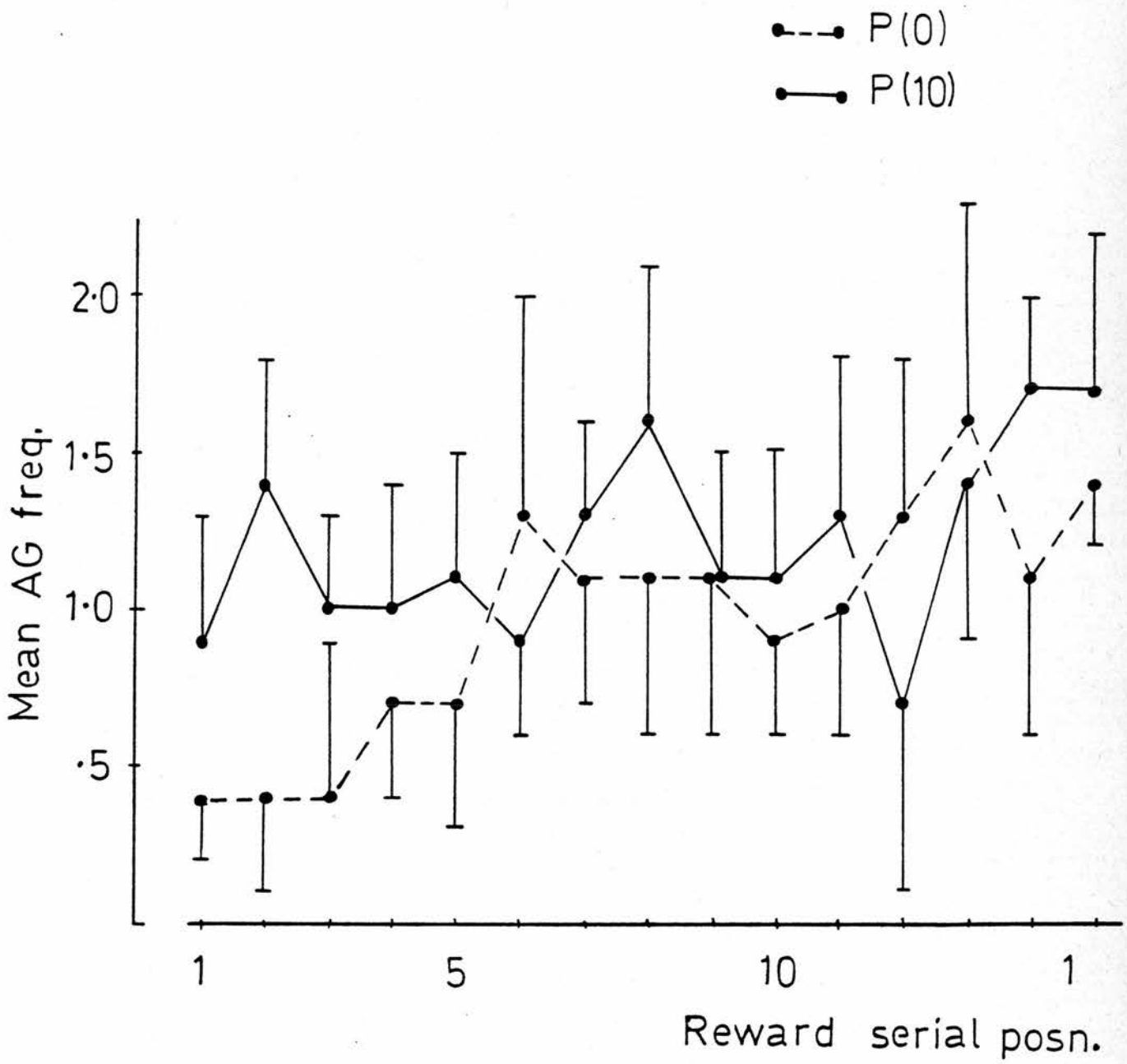

P(0)
P(10)
2·0
1·5
1·0
·5
Mean AG freq.
1
5
10
1
Reward serial posn.

Figure 88

The course of mean lateral display duration (LD(d)) over successive rewards in sessions with 0 mins. priming (P(0)) and 10 mins. priming (P(10)). Bars represent one standard error. N = 8.

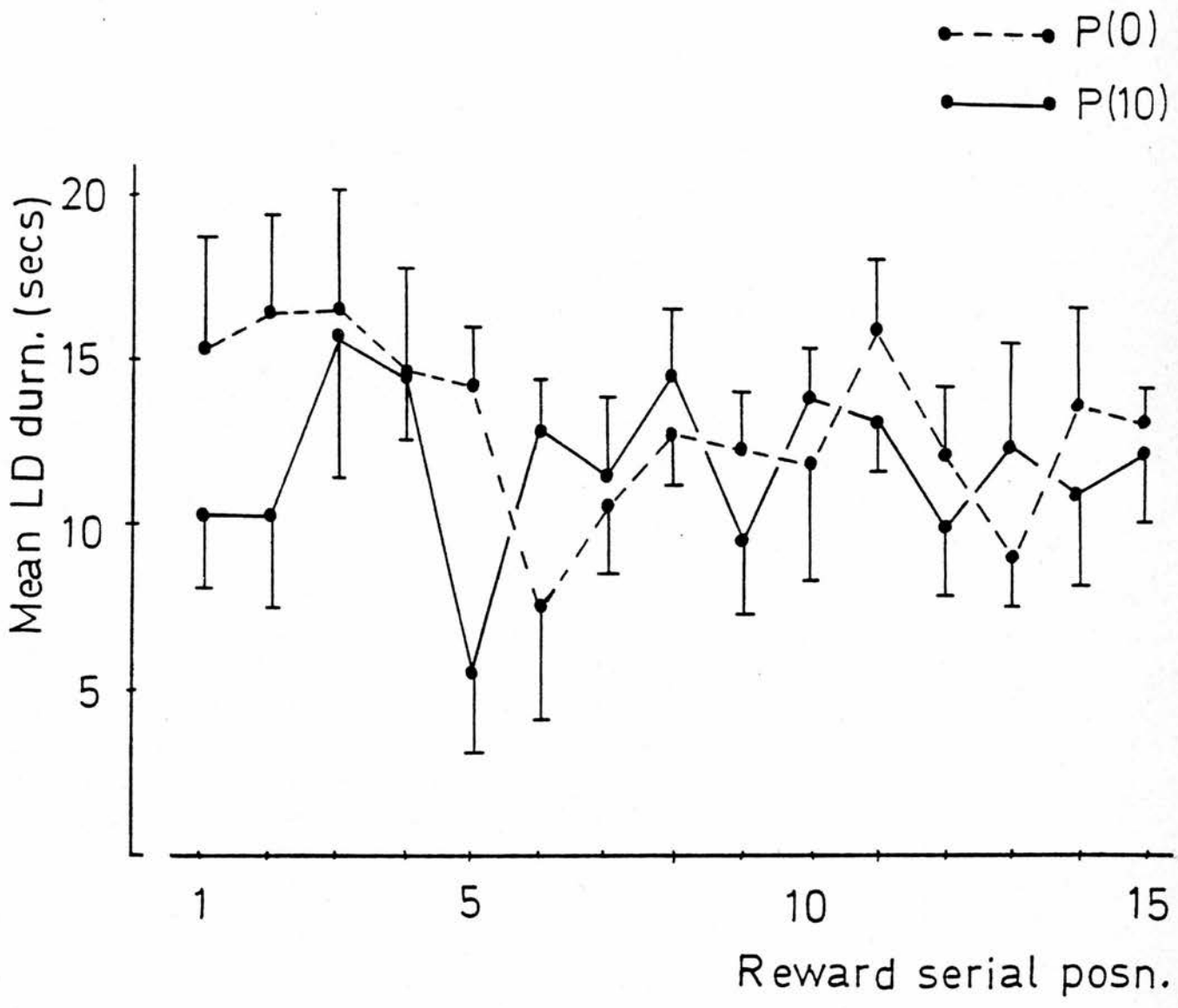

P(0)
P(10)
Mean LD durn. (secs)
20
15
10
5
1
5
10
15
Reward serial posn.

Table 31

The Spearman correlations between susceptibility to priming and unprimed inter - response intervals (1 - tailed significance testing), N = 8.

"Natural priming"

(a)	F5(0)	vs	dP(0)	rho = .952 $p < .01$
(b)	F5(0)	vs	pP(0)	rho = .813 $p < .05$

"Priming procedures"

(c)	F5(0)	vs	dP(10)	rho = .881 $p < .01$
(d)	F5(0)	vs	pP(10)	rho = .857 $p < .01$
(e)	F5(0)	vs	dP(10)	rho = .643 $p < .05$
(f)	F5(0)	vs	pP(15)	rho = .643 $p < .05$

F5(0) is the mean of the first 5 IRI's of the 0 mins. priming condition.

dP(0) is the difference between the mean of the first and last 3 IRI's of the 0 mins. priming condition.

pP(0) is the proportionate change between mean first and last 3 IRI's.

dP(10) is the difference between the mean for first 3 IRI's of the 0 mins. priming condition, and the mean for the first 3 IRI's of the 10 min. priming condition.

Table 32

Comparison of the mean rates of post-reward behaviours for the first 3 (F3) and last 3 (L3) inter-response intervals (IRI's) of 0 and 10 min. priming conditions (P(0) and P(10)). Significance testing was by Wilcoxon test.

Rates	F3 P(0)vsP(10)	L3 P(0)vsP(10)	P(0) F3 vs L3	P(0) F3 vs L3	Priming Effect?
Wls(f)	T = 4 N = 7 p > .05	T = 9 N = 7 p > .05	T = 4 N = 7 p > .05	T = 4 N = 6 p > .05	No.
Wls(d)	T = 10 N = 7 p > .05	T = 12 N = 7 p > .05	T = 5 N = 6 p > .05	T = 8 N = 6 p > .05	No.
SeS(d)	T = 12 N = 7 p > .05	T = 4 N = 7 p > .05	T = 10 N = 7 p > .05	T = 5 N = 7 p > .05	No.
SeD(d)	T = 12 N = 7 p > .05	T = 6 N = 7 p > .05	T = 8 N = 7 p > .05	T = 8.5 N = 7 p > .05	No.
Op - Rf	T = 5 N = 6 p > .05	T = 0 N = 6 p > .025	T = 3* N = 7 p > .05 (2-tailed)	T = 4.5 N = 6 p > .05	?
Wi	T = 2* N = 6 p < .05 (2-tailed)	T = 8 N = 6 p > .05	T = 4 N = 7 p > .05	T = 0 N = 6 p < .025	?
Ap	T = 0* N = 6 p < .05 (2-tailed)	T = 6 N = 5 p > .05	T = 4 N = 5 p > .05	T = 0 N = 6 p < .025	?

Absolute amounts	F3 P(0)vsP(10)	P(10) F3 vs L3	Priming effect?
Wi	T = 8.5 N = 6 p > .05	T = 3 N = 5 p > .05	No.
Ap	T = 5 N = 5 p > .05	T = 0 N = 5 p < .05	?

* indicates that the difference was not in the predicted direction. In such a case, 2 - tailed probabilities are given.

? indicates a complex effect not readily attributable to priming. See discussion in Ch. 11.5(b).

Table 33

The course of biting over successive rewards in sessions with 0 mins. priming (P(0)) and 10 mins. priming (P(10)).

P(10) N = 7

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\bar{X}$	0	0	0	0	.14	0	.29	0	.14	.14	.14	.14	0	.14	0
SEM	0	0	0	0	.15	0	.20	0	.15	.15	.15	.15	0	.15	0

No. of subjects showing biting = 4

P(0) N = 7

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\bar{X}$	0	0	0	0	0	0	0	0	0	.14	.14	0	0	0	0
SEM	0	0	0	0	0	0	0	0	0	.15	.15	0	0	0	0

No. of subjects showing biting = 1

Table 34

The course of butting frequency (Bu(f)) over successive rewards in sessions with 0 mins. priming (P(0)) and 10 mins. priming (P(10)).

P(10)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\bar{X}$	0	0	.29	0	.14	,14	.43	.14	.14	.57	.29	.29	.57	.43	.14
SEM	0	0	.20	0	.15	.15	.32	.18	.15	.32	.31	.31	.46	.22	.15

No. of subjects showing butting = 5

P(0)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$\bar{X}$	0	0	0	0	0	0	0	0	0	.14	0	0	0	0	0
SEM	0	0	0	0	0	0	0	0	0	.15	0	0	0	0	0

NO. of subjects showing butting = 1

Table 35

Comparisons of the mean amounts of reward-elicited behaviours for the first 3 (F3) and last 3 (L3) rewards in the 0 mins. and 10 mins. priming conditions (P(0) and P(10)).

Significance testing was by Wilcoxon test (1-tailed).

	F3	L3	P(0)	P(10)	
	P(0)vsP(10)	P(0)vs (10)	F3 vs L3	F3 vs L3	Priming Effect?
LD(d)	T = 1 N = 7 p < .025	T = 9 N = 7 p > .05	T = 2 N = 7 p < .025	T = 13.5 N = 7 p > .05	Yes
AG(f)	T = 0 N = 6 p < .025	T = 13 N = 6 p > .05	T = 0 N = 6 p < .025	T = 4 N = 6 p > .05	Yes

CHAPTER 12

12.1 The Effect of "Time-Out" After Training on Resistance to Extinction

12.1 (a) Introduction

The experiment to be reported investigates the control of operant responding in extinction exerted by the motivational after-effects of previous rewards. To determine the relations between these after-effects and operant responding, a "time-out" period is interposed between the beginning of extinction and the end of the preceding session of training. As the duration of this time-out period is increased, so the operant response motivating after-effects of rewards which have survived into extinction should decrease. Thus the interposition of a time-out should decrease resistance to extinction.

12.1 (b) Subjects

Six male Betta splendens were randomly selected from those already conditioned to perform operant responses for display reward and which were responding at a stable daily rate. None of these subjects had ever experienced extinction or any reinforcement schedule other than continuous reinforcement (CRF). These 6 fish acted as experimental subjects.

Since a control group is required because of the possibility of heightened activity due to reward which may persist into extinction and since male Bettas become sluggish if left for long periods without social interaction, control subjects should have had as much agonistic experience as experimental subjects, but no conditioning experience. This could be achieved by randomly selcting experimental and control fish, training the experimental group, and by using a yoked control method (e.g. Goldstein, 1967) give both

groups an equal number of exposures to stimulus fish at the same intervals. For technical reasons, such a method could not be used in the present experiment, so a less satisfactory alternative was devised.

From the same stock of fish from which experimental subjects were selected, 6 control fish with nest volumes less than .4cms.^{3} were randomly chosen. Displaying stimulus fish were assigned to these males by the same method as was used to assign stimulus fish to experimental subjects. Control fish were then randomly paired with experimental subjects. Control fish and their stimulus males were moved to experimental maintenance conditions.

12.1 (c) Apparatus

The apparatus described in 6.2 was modified in the following way. The flat plexiglass bar supporting the brass rod and response gate was unbolted from the test-chamber lid. By lifting the bar, the response gate could then be moved vertically, lifting it clear of the subject's tank. This allowed operant responding in the subject to be prevented, while being minimally disturbing in its effects. To maintain the orientation of the response gate in the horizontal plane, a guide was constructed. This consisted of 4 flat vertical bars of plexiglass. These were in pairs and fixed so that the bar from which the response gate was suspended could move only in the vertical plane. To the centre of this bar was connected a length of cord which ran vertically through a ring in the test cubicle and out of an aperture in its back wall.

This above modification meant that by pulling the cord protruding from the cubicle back wall, the operandum could be raised out of the subject's tank while the test chamber lid remained closed. On the back wall of the cubicle was a

hook on which the cord could be located by means of a ring attached to its end. This held the response gate in the "up" position.

12.1 (d) Method

This experiment compared the number of responses in extinction which occurred after "time-out" periods of different duration. Time out (T.O) refers to a period between the last rewarded response and the beginning of extinction, during which no responses were allowed to occur (the response gate was removed). Lest any effect of T.O. duration found, be caused not by operant response-related motivation and its decay, but by differences in general activity occurring at different times after termination of the last reward, a control group was required. This control group was tested in a pseudo-extinction condition, which followed a session in which the number of non-contingent presentations ("rewards") which occurred was equated with the number earned by the subject to which the control fish was assigned.

The operant behaviour of experimental fish was recorded on a CRF schedule until at least 4 consecutive daily sessions of responding with the same stimulus fish showed that response rate was stable. The last session of this block of stable responding was termed the pre-test session. After this session a 1hr. extinction session was administered with responses not being followed by reward. The number of responses in this extinction session was recorded. On the days following extinction, fish were reconditioned until at least 4 consecutive sessions occurred over which response rate was judged stable. Again, the last session of the block of 4 stable sessions was the pre-test session and was followed by extinction as before. This was again followed by daily retraining sessions, a further 4 sessions of stable responding and a further extinction period. Thus, experimental

subjects had 3 sessions of extinction, each preceded by a pre-test session which was the last of a block of 4 stable sessions. The first and second extinction tests were followed by reconditioning. Between the last reward of pre-test sessions and the beginning of extinction sessions, a period was interposed during which operant responses could not occur. This period of "time-out" (T.O.) was of 0, 30 or 60mins. duration, and these 3 conditions were termed E0. E30 and E60 respectively. Each subject was tested with each of the 3 T.O. durations. The order in which the different T.O. conditions were applied was counterbalanced across subjects in a pseudo-randomized block design.

For at least 7 consecutive days before testing, control fish were presented in their home tanks with their assigned stimulus fish. Presentation was in a standard stimulus fish container and lasted for 15mins. 1 control subject produced submission in its stimulus fish and that stimulus was replaced from stock. The reason for these stimulus presentations to control subjects was not to attempt to equate their daily amount of display with that of experimental subjects, but to ensure that they did not become sluggish due to protracted periods of social isolation.

The only attempt to equate periods of display for experimental and control fish was in each pre-test session of experimental fish. For each experimental subject, the number of rewards and the mean inter-reward interval during a particular pre-test session were calculated. The control fish for that subject was then in the test chamber automatically presented with its stimulus fish the same number of times and at the mean inter-presentation interval of the subject to which it was assigned. Thus, immediately before their T.O. and extinction procedures, experimental and control subjects had comparable amounts of display to their respective stimulus fish. The control fish was therefore treated with the same T.O. and "extinction" procedures as the experimental fish

assigned to it, and the number of responses it produced in each "extinction" was recorded. Because of the need for equalization of pre-test display in experimental and control fish, experimental subjects had to be tested before their controls. Each subject-control pair was tested at the same time of day, but controls on the day after experimental fish. The first response of extinction which initiated the session, was not included in analysis.

12.1 (e) Procedure

The preliminary procedure for both experimental and control fish, including stimulus pre-treatment and pre-feeding, was the same as for the previous experiment. Immediately before conditioning sessions, experimental fish were pre-treated to supress courtship behaviours as in previous experiments. Before pre-test sessions (the sessions immediately preceding time-out and extinction) both experimental and control fish were pre-treated in this way.

For experimental fish, the pre-test sessions, begins in the same way as previous conditioning sessions. However, the session is not terminated after 30mins. (excluding reward time) as before. Instead, the session ends with the first reward after 30mins. have elapsed. It is during this reward, 10secs. after its initiation, that the response gate is removed from the subject's tank. This is accomplished by the experimenter gently pulling the cord which raises the response gate clear of the water. A cut-out switch is then thrown to prevent any registration of responses while the response gate is being disturbed. It is then held in this position by locating its attached ring to the hook provided. Because the last reward of the pre-test session is still in progress at this point, and subject and stimulus fish are displaying, removal of the response gate causes no perceptible disturbance in the subject.

The time-out period begins with the end of the reward during which the response gate is withdrawn, and during T.O. the test chamber remains illuminated. After the beginning of time-out, no further rewards can be earned by subjects until reconditioning on the following day. When the T.O. period has ended (timing is by Smith's mechanical timer) the manipulandum is very gently lowered into the subject's tank and reactivated by throwing the cut-out switch. No fright responses were ever observed as a result of this procedure. Operant responses are now recorded but no rewards are delivered. This extinction session lasts 60mins. from the first unrewarded response of the subject. If the T.O. period is 0 secs., the response gate is still removed after 10secs. of the last reward of the pre-test session, but is reintroduced simultaneously with the termination of that reward. During extinction the stimulus fish in its container and the stimulus cover remained in place. No formal behavioural observations were made during this experiment with one exception. At the end of extinction tests in every condition a 1min. stimulus presentation was given and the number of withdrawals counted. This allowed some estimation of the degree to which sexual tendencies had become dominant during the long periods of non-reward. Since all experimental and control fish could not be tested in a single day, the experiment was carried out in three segments and in each segment 2 experimental and their 2 control fish were tested.

12.2 Gross Effects

Only one fish showed any withdrawal (one) during post-extinction stimulus presentations. An increase in sexual tendencies with non-reward could not therefore explain any of the effects of time-out which emerged. The results of comparisons of the total numbers of responses in extinction in the 3 T.O. conditions, E0, E30 and E60 are shown in

Fig. 89. The experimental group shows a significant effect of T.O. (Fried., $p<.01$) with the E0 condition producing approximately twice the number of responses shown in the E10 condition. The control group showed no significant effect of T.O. duration (Fried., $p=.956$). The effect of T.O. duration on resistance to extinction cannot therefore be attributed to a decrease in general activity after time-out.

12.3 Intra-Session Effects

Fig. 90(a) shows that for the experimental group in all T.O. conditions mean responses per successive 10 minute interval of extinction decreased. Only in the E0 group was this decrease within the extinction condition significant (Fried: E0, $p<.01$; E30, $p>.10$; E60, $p>.10$). In the control group, all T.O. conditions produced a higher mean number of responses in the first 10mins. of "extinction", while responding stayed at a stable level thereafter (Fig. 90(b)) Only in the E60 condition did control fish show a significant change in responding over the session (Fried., $p<.01$). The significant decrease in responding into control E60 sessions may be due to a higher response rate at the beginnings of sessions and a lower rate at the ends. Because this condition involves the longest T.O. duration, this initially higher level of responding in the E60 condition is not likely to be due to heightened activity caused by pre-test presentations. Instead it may be that during the 60mins. time-out period, some dishabituation to the presence of the response gate occurred, so that the beginning of "extinction" involved some exploratory activity.

12.4 The Effect of Repeated Extinctions and Relations Between the Training Conditions and Resistance to Extinction

Table 36 shows the mean numbers of responses (and rewards) in pre-test sessions for experimental subjects in each

condition. The number of responses (rewards) occurring in pre-tests does not differ significantly across T.O. conditions (Fried., p=.57). Also shown in Table 36 are the mean numbers of rewarded responses which occurred in all conditioning sessions preceding each extinction. No significant differences were found between T.O. conditions in the conditioning history of subjects (Fried., p=1.00)

Table 37 shows that no significant Spearman correlations were found between the number of responses in extinction and the number of rewarded responses in the pre-test. In addition, no significant correlations were found between the number of responses in extinction and the total number of rewarded responses before extinction. These results were found when all conditions were pooled (N=18) and when individual extinction conditions were considered separately (N=6, for each T.O. condition). The differences between T.O. conditions cannot therefore be accounted for by differences in their pre-test performance or in their total conditioning history.

Table 37 also shows that there were no significant differences between the numbers of responses in extinction due to the serial position of the extinction session (Fried., p=.956). That is not to say that successive extinctions do not produce progressively fewer responses in display rewarded Bettas, but that the effect of extinction session serial position is minor compared to that of the duration of time-out before extinction.

12.5 Discussion

Resistance to extinction in dsiplay rewarded Betta splendens is substantially reduced by interposing a time-out between the last rewarded response of conditioning and the beginning of extinction. This effect cannot be accounted for by differences beteen time-out conditions in the total

number of rewarded responses in training, the number which occurred in the session immediately preceding extinction, or the serial position of extinction sessions. Furthermore, only one subject ever showed a tendency to behave sexually to the stimulus after extinction. Extinction effects cannot therefore be attributed to the disinhibition of sexual tendencies. The effect of time-out on resistance to extinction may be interpreted as due to the decay of reward-induced motivation during time-out periods. That reward-induced motivation is a major determinant of responding in extinction is indicated by the result that a 60min. time-out period reduced the number of responses by 50%, and that with 30 and 60 min. time-out periods, no significant decline in responding occurs during extinction tests. This latter result in particular means that when reward induced motivation has decayed, the remaining sources of motivation to respond are comparatively weak.

This dependence of responding in extinction on the motivational after-effects of reward may have implications for the comparison of reward-types in the resistance to extinction they produce. Hogan (1967, 1978) compared resistance to extinction in food and display rewarded male Bettas and found markedly faster extinction after display reward. Resistance to extinction in food rewarded animals is positively related to deprivation (Bolles, 1975) and the present results show that resistance to extinction after display reward is negatively related to time-out after conditioning. Hogan's (1967) experiment involved the separation of conditioning and extinction sessions by one day. The motivating after-effects of reward would therefore have ample time to decay before extinction, while food rewarded animals would remain in a state of deprivation. It might be expected that most of the responding for display occurring after a 24hr. time-out, would be motivated by cues signalling the onset of a new session. It would also be expected that even if no time-out occurred between conditioning with display

reward and extinction after this reward, motivation would be decaying, while after food it would (if anything) be increasing during extinction. The possibility of decaying after-effects in the food intake control system will be investigated in the next chapter.

Possibly related to the effect of time-out on resistnace to extinction in display rewarded Bettas is the finding by Baenninger and Mattelman (1973) of a slower rate of extinction than expected from the results other experiments (e.g. Hogan, 1967) when a display eliciting mirror was continuously available during extinction. These authors did not, however, directly compare extinction with and without a continuously available mirror.

Since a fixed ratio (FR) reinforcement schedule involves the repeated performance of the response before a reward is administered, the minimum inter-reward interval (IRI) which can occur is increased. If reward induced motivation decays between reward, then it would be expected that as this minimum IRI increases (increases in FR) the motivation to perform operant responses would decline. The following experiment investigates the relations between FR schedule and the intrasession patterning of operant responding.

12.6 The Effect of Fixed Ratio Schedule on Operant Performance

12.6 (a) Method

Five subjects and their stimulus fish were randomly selected form those already trained to perform operant responses for display reward. Some of these subjects had been used in previous experiments. No subject had ever experienced any reinforcement schedule other than that of continuous reinforcement (CRF) nor been subject to extinction.

Each subject was tested on an ascending series of fixed ratio schedules from FR1 (CRF) to FR10, being returned thereafter to FR1. The return to FR1 acted as a control for changes in performance not due to FR schedule. If a subject

showed ratio strain, it was not moved up to the next FR schedule but was instead returned to FR1. Ratio strain was defined as having occurred if no responses were produced in 20 consecutive minutes of a session. Each subject was kept on each schedule until 4 consecutive daily sessions had elapsed over which responses per session were judged stable. Only the data from those 4 stable sessions at each ratio were used in analysis. Although behavioural observations were made during sessions, observational data will not be reported here. The analysis of response data was by the following means:

a) The mean number of responses was calculated for each subject over the 4 stable sessions at each ratio.

b) The change in responding over sessions was described for each subject. Over each stable session of each subject, the mean number of responses in each 5min. segment of the session was calculated. This was performed separately for each ratio. The change into the session was then expressed as an "advantage" score, by subtracting the mean number of responses in the first segment from the mean number in the last segment. If the resulting difference was positive, it indicated an increase in responding into the session. If it was negative, response rate had declined. A similar procedure was used to express the change in responding from the first 5mins. to the 3rd 5mins. of sessions (mid-session advantage). As for previous operant experiments, the first response of each session was omitted from data analysis.

Since subjects show ratio strain at different fixed ratios, no statistical analysis of these data was carried out.

12.6 (b) Apparatus

The apparatus was the same as used in previous experiments

but set so as to deliver reinforcements only after the required numbers of responses had been detected. The response counter reset automatically after each response run was completed and reward delivered.

12.6 (c) Procedure

Preliminary procedures, including stimulus and subject pre-treatment, were the same as for previous operant experiments. The only change in procedure was that instead of sessions being terminated 30mins. after the first response (exclusive of time consumed by reward) sessions were continued after 30mins. had elapsed if the last response was not a rewarded response. The session continued until the current response run was completed and reward delivered.

12.7 Results

Fig. 91 shows the mean number of responses over 4 stable sessions for each subject at each fixed ratio. It can be seen that ratio strain occurred for 1 subject at FR3, another at FR4, one at FR7 and one at FR8. Only a single subject remained responding consistently at FR8. It can also be seen that the number of responses produced by 4 of the 5 subjects gradually decreased before ratio strain occurred. When subjects were returned to FR1, 4 out of 5 of them showed fewer responses than during their first FR1 session.

Figs. 92 and 93 show the mean mid-session and end of session advantage respectively, for each subject as FR was increased. Considering first mid-session advantage, it can be seen to be positive at FR1, then decreases for every subject, becoming negative in every case before ratio strain occurs. On return to FR1, 4 out of 5 subjects return to a positive mid-session advantage. Considering the end of

session advantages, again all subjects began with a positive advantage at FR1, becoming negative as FR is increased. In this case, every subject shows a non-negative end of session advantage when returned to FR1.

Fig. 94 shows the course of the mean number of responses over successive 5min. segments of sessions at FR1 (first time) FR2 and FR10 for a single subject. This was the only subject to maintain responding until FR10, but its intra-session pattern of responses is representative. At FR1, it increased its response rate into the session, at FR2, an increase also occurred, but was slight, and at FR10 response rate declined in sessions.

12.8 Discussion

Increases in fixed ratio requirement were accompanied by a decrease in responses per session for most subjects, until ratio strain occurred. On return to FR1, subjects did not completely regain their former level of responding. Whether this is a consequence of habituation to the reward stimulus, or to other factors is not clear. A result found for every subject was that as ratio requirement was increased, the facilitation which occurred into sessions at FR1 disappeared, becoming negative in that an intra-session decline in responding occurred. On return to FR1, all subjects returned to a non-negative intra-session facilitation of responding (when the end of session advantage was considered).

That ratio strain (as defined in this experiment) followed a gradual decrease in intra-session facilitation of responding, suggests that these effects are similar in causation for display rewarded Bettas. Thus, ratio strain may be an extreme form of the decline in responding shown at higher fixed ratios.

The finding that the imposition of FR schedules reduces then eliminates the increase in responding which occurs into

FR1 sessions is consistent with the hypothesis that any experimental manipulation which serves to increase inter-reward intervals will decrease the motivation to perform operant responses. Since responding on the higher FR schedules not only failed to increase within sessions but actually decreased, some motivation other than the effect of rewards must be present at the beginnings of sessions. It may be that subject pre-treatment provided this stimulation, but it is difficult to accept this as a full explanation since in this experiment no subject ever required more than 1min. of such pre-treatment. In addition, even when no pre-treatment is given subjects begin a session by performing a response without previous stimulation on that day. The most plausible hypothesis to account for is that the experimental situation itself becomes a set of conditioned stimuli with response motivating properties. This situation-induced motivation may not last for long after the session begins since the previous experiments showed that a time-out, even after a session of reward, leaves little motivation to perform operant responses.

The results of this experiment are in agreement with those of Hogan (1978) who found that when a fixed ratio requirement was imposed on subjects, the percentage of the total number of responses which occurred during the first halves of sessions increased from 57% at FR1 to 62% as the ratio was increased.

Since the major sources of motivation to perform operant responses for display reward are induced by the reward itself, and since these decay during inter-reward intervals, it is difficult to see how such a system could be expected to support compensation for FR schedules (c.f. ch. 1). Without the action of an additional depletion-repletion or "amount monitoring" system, the imposition of an FR schedule, since it increases minimum inter-reinforcement interval, could only act to reduce motivation to respond.

For Betta splendens, no effect of deprivation of aggression on operant responding has been found (Hogan, 1978). Only in juvenile damselfish (Microspathodon chrysurus) responding for display reward, has any effect been shown which could be interpreted in deprivation terms (Rasa, 1971), an alternative interpretation, however, of these results in terms of dishabituation to the stimulus between presentations, has been advanced (Heiligenberg and Kramer, 1972). In addition, even if an isolation induced increase in aggressiveness does occur in damselfish, there is no evidence to suggest that the mechanisms underlying this exist in male Betta splendens. The failure of display rewarded Bettas to compensate for increases in FR requirement while they do show compensation for food, has been discussed (ch. 1.6(?)). Questions about this difference have usually centred on the problem of why no compensation for display occurs. However, it is difficult to account for the absence of a phenomenon, unless those factors are understood which control it when it does occur. The following experiment investigates the control of food intake and its response to FR schedules in the Barbary dove (Streptopelia risoria).

Figure 89

The mean number of responses in extinction as a function of time-out (T.O.) duration for experimental (E) and (c) control fish. Bars indicate 2 standard errors.

Significance testing by Friedman 2 - way analysis of variance.

Experimental group

T.O.(mins.)	0	30	60
$\bar{X}$	43.17	25.33	22.67
SEM	8.88	4.80	5.57
Total Ranks	18	9	9

Chi = 9.00
k = 3, N = 6
p < .01
ω = .7500

L = 81, p = .01

Control group

T.O.(mins.)	0	30	60
$\bar{X}$	9.50	6.67	9.83
SEM	2.97	2.66	1.93
Total Ranks	13	11	12

Chi = 0.33
k = 3, N = 6
p = .956
ω = .0278

L = 73, p > .05

Figure 90 (a)

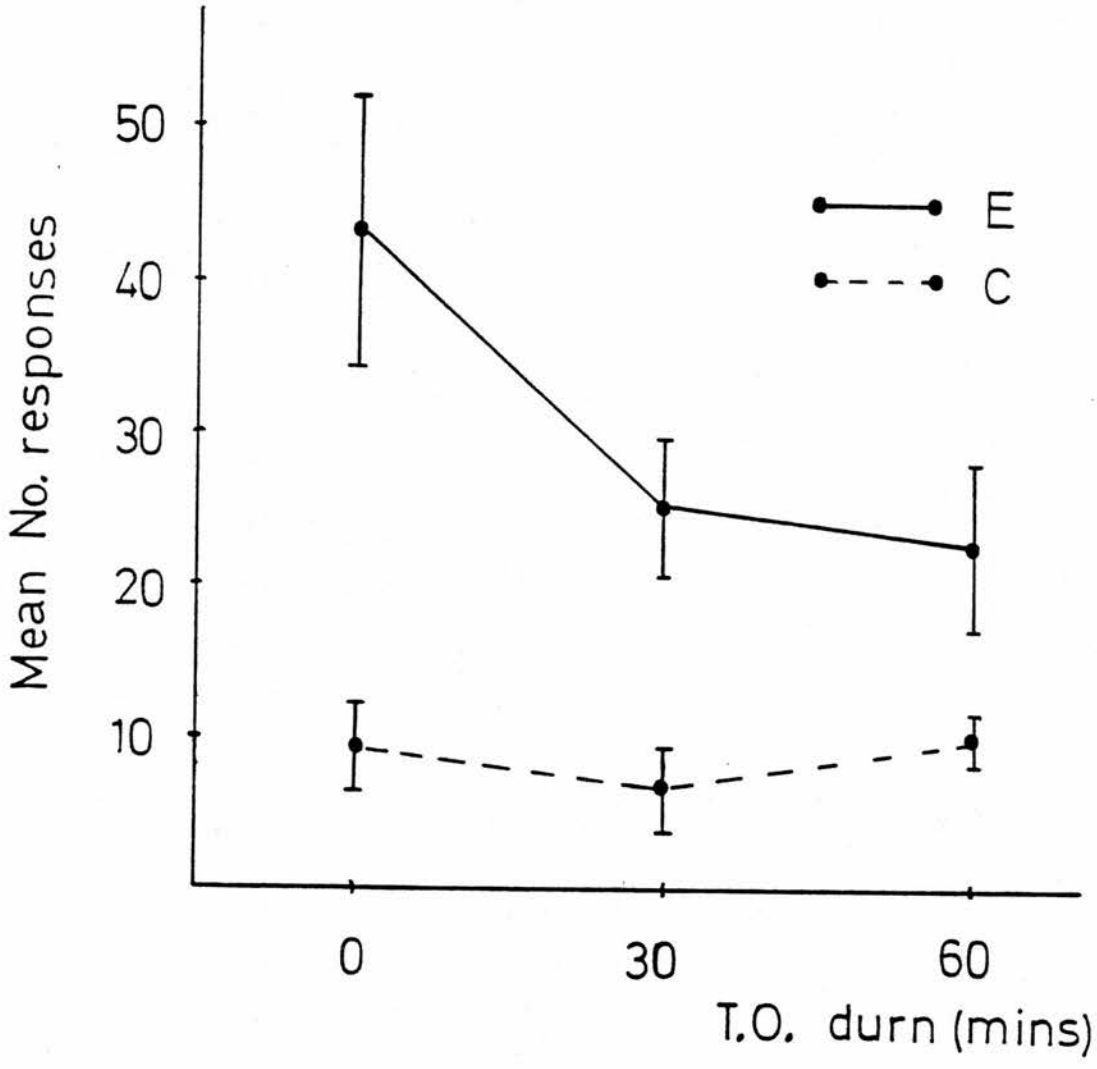
Mean responses per successive 10 min. segments of extinction in the three time-out (T.O.) conditions (E0, E 30 and E60) for the experimental group..

T.O.(mins.)		0-10	11-20	21-30	31-40	41-50	51-60
E0	$\bar{X}$	14.00	9.00	5.33	7.00	3.67	4.17
	SEM	2.02	2.65	2.36	2.65	1.04	1.14
	Total Ranks	33.0	29.5	16.5	21.0	15.0	11.0
E30	$\bar{X}$	7.00	4.33	2.50	5.00	3.17	3.33
	SEM	1.85	.61	.88	1.64	1.21	1.00
	Total Ranks	28.5	24.5	13.5	25.0	16	18.5

Chi = 17.7380 ω = .5913
df = 5, N = 6
p < .01

L = 515.5
p < .001

(continued overleaf)


Mean No. responses
50
40
30
20
10
E
C
0
30
60
T.O. durn (mins)

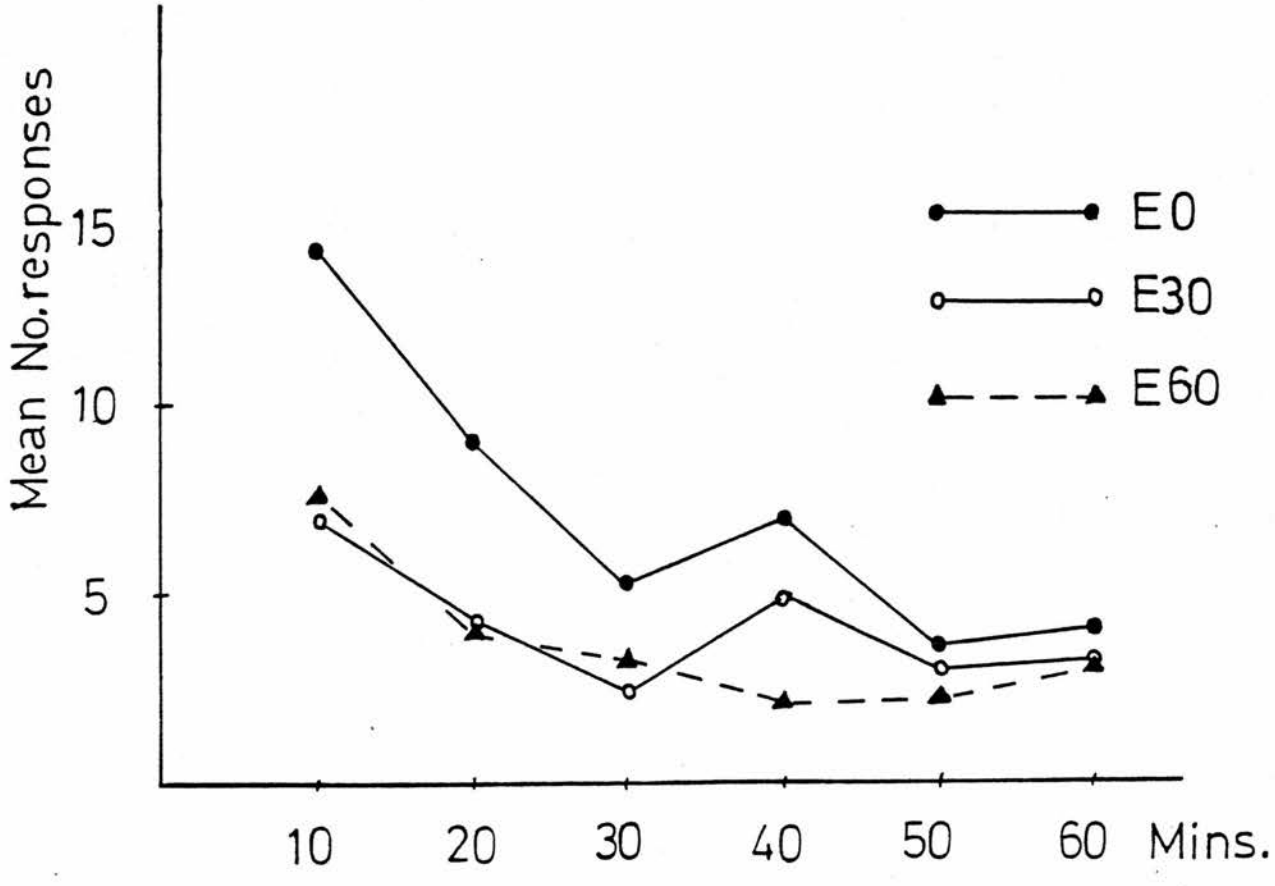

Mean No.responses
15
10
5
E0
E30
E60
10
20
30
40
50
60
Mins.

Figure 90 (a) continued

E30 Chi = 8.1904 $\omega = .2730$ $L = 473$
df = 5, N = 6 $P > .05$
p > .10

E60	0-10	11-20	21-30	31-40	41-50	51-60
$\bar{X}$	7.67	4.00	3.33	2.17	2.33	3.17
SEM	2.25	1.65	1.12	0.17	.88	1.14
Total Ranks	31.5	22.5	20.5	15.5	17.5	18.5

Chi = 7.6904
df = 5, N = 6 $L = 483.5$
p > .10 $P < .05$
$\omega = .2565$

Figure 90(b)

The course of mean responses per successive 10 mins. of "extinction" in the three time-out conditions (EC0, EC30, EC60) for the control group. Significance testing was by Friedman analysis of variance.

T.O.(mins.)		0-10	11-20	21-30	31-40	41-50	51-60
0	$\bar{X}$	3.00	1.00	1.83	1.17	1.33	1.17
	SEM	1.65	0.69	0.52	0.72	0.46	0.72
Total Ranks		23.5	19.0	24.5	18.5	21.0	19.5

Chi = 1.4762 $\omega = .0492$ $L = 451, p > .05$
df = 5
$p > .90$

		0-10	11-20	21-30	31-40	41-50	51-60
30	$\bar{X}$	2.50	0.67	.67	1.00	1.50	0.33
	SEM	1.43	.36	.36	.56	.62	.23
Total Ranks		26.00	19.00	18.5	20.00	27.00	15.5

Chi = 4.8809 $\omega = .1627$ $L = 454.5, p > .05$
df = 5
$p > .30$

		0-10	11-20	21-30	31-40	41-50	51-60
60	$\bar{X}$	3.83	1.83	1.33	1.83	.67	.33
	SEM	.77	.66	.83	.66	.36	.36
Total Ranks		33.00	26.0	20.5	21.5	14.0	11.0

Chi = 15.1666 $\omega = .5056$ $L = 513.5, p < .001$
df = 5
$p < .01$

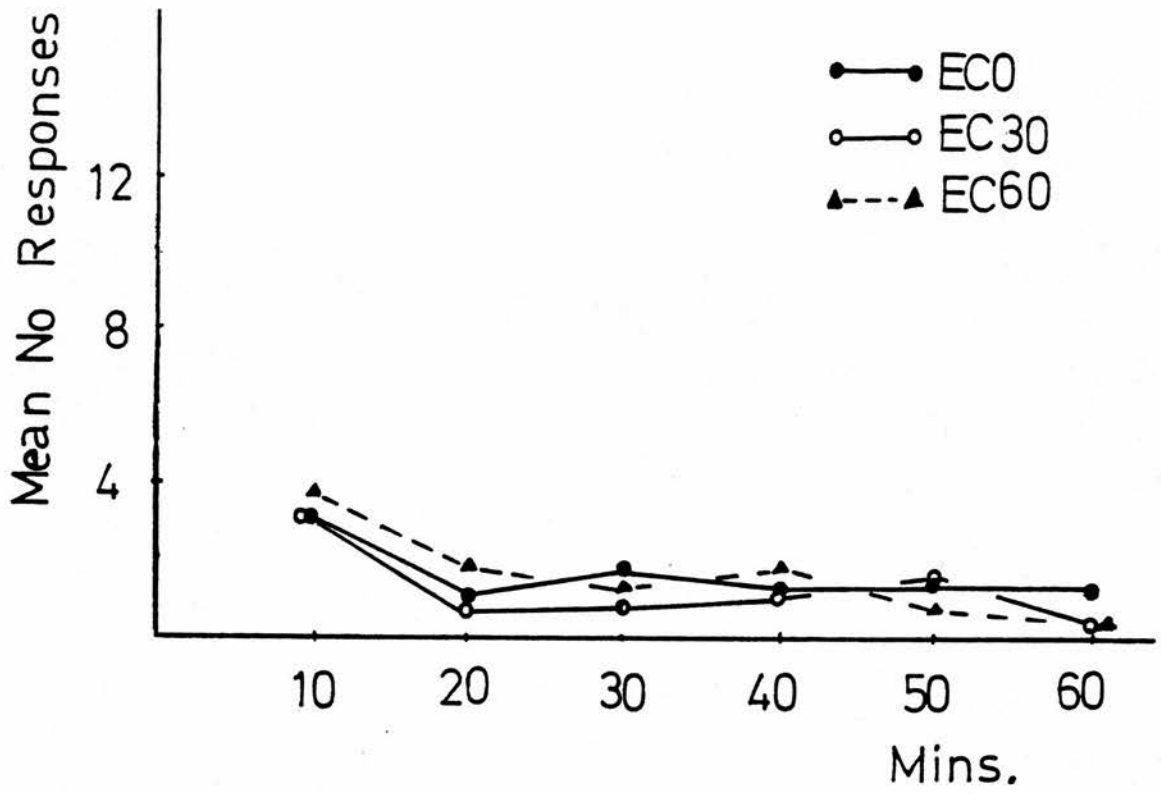

Mean No Responses
12
8
4
EC0
EC30
EC60
10
20
30
40
50
60
Mins.

Figure 91

The mean number of responses for each subject in sessions at each fixed ratio (FR) schedule.

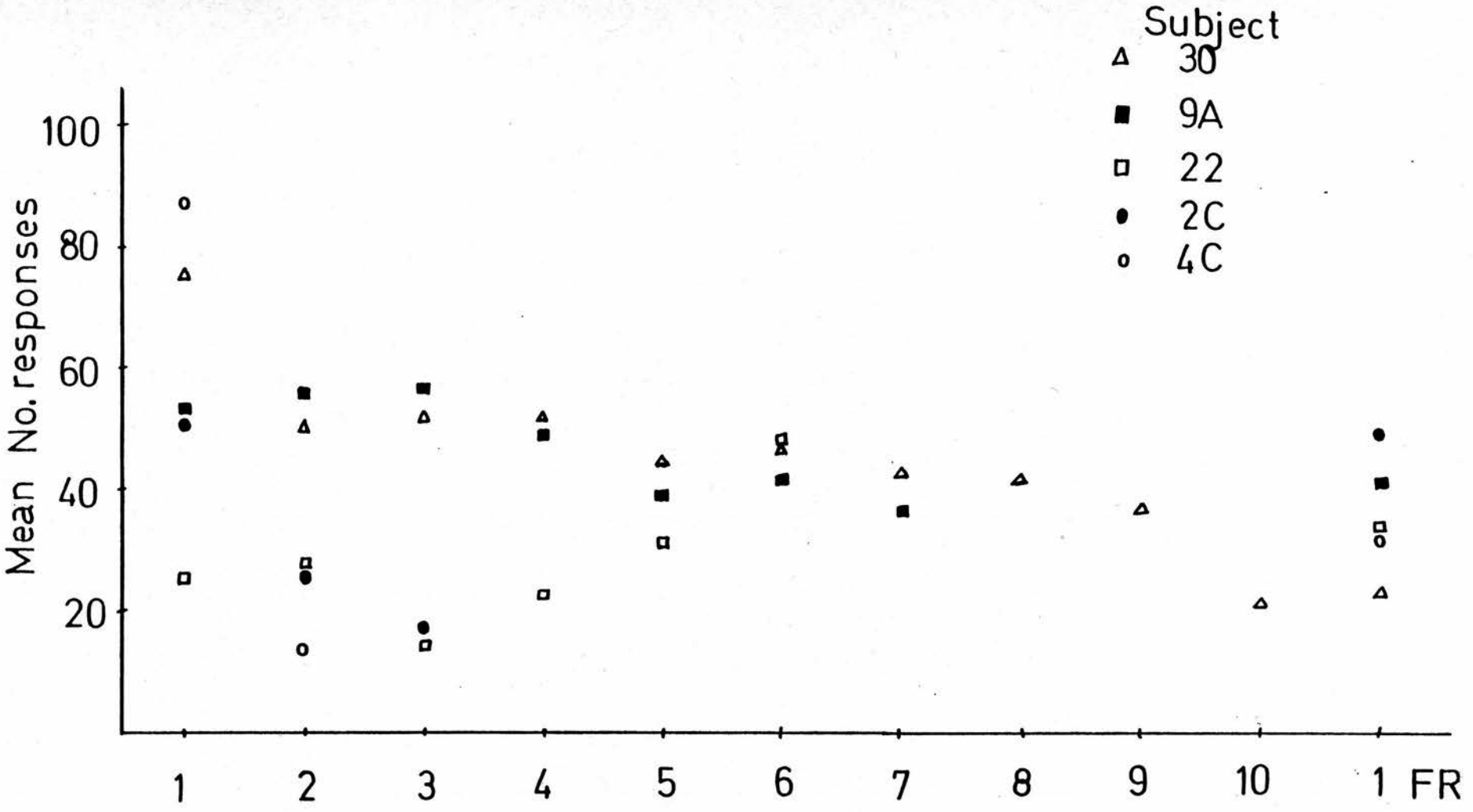

Subject
30
9A
22
2C
4C
Mean No. responses
100
80
60
40
20
1
2
3
4
5
6
7
8
9
10
1 FR

Figure 92

The mean mid-session advantage for each subject at each fixed ratio (FR).

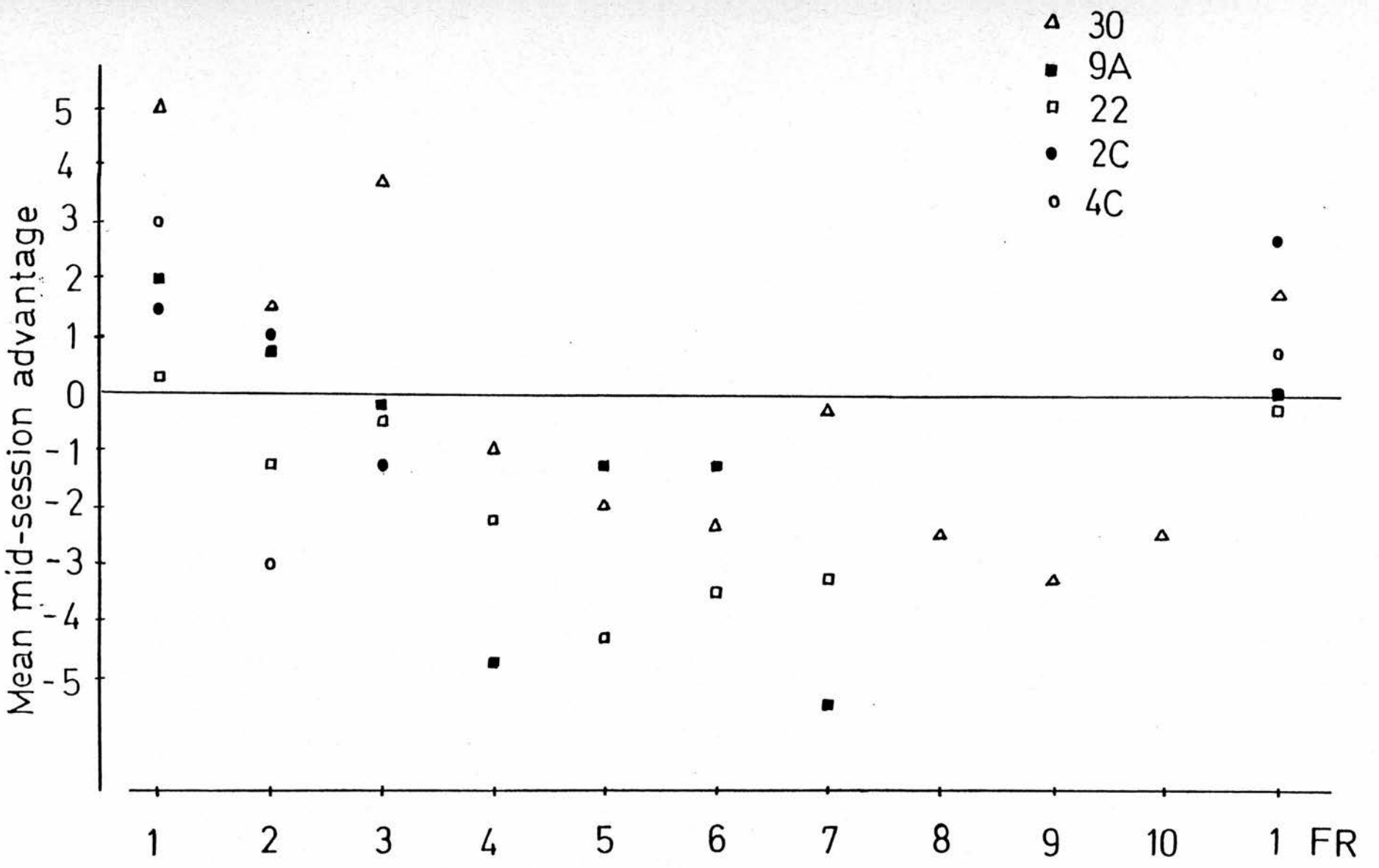

30
9A
22
2C
4C
Mean mid-session advantage
5
4
3
2
1
0
-1
-2
-3
-4
-5
1
2
3
4
5
6
7
8
9
10
1 FR

Figure 93

The mean end of session advantage for each subject at each fixed ratio (FR).

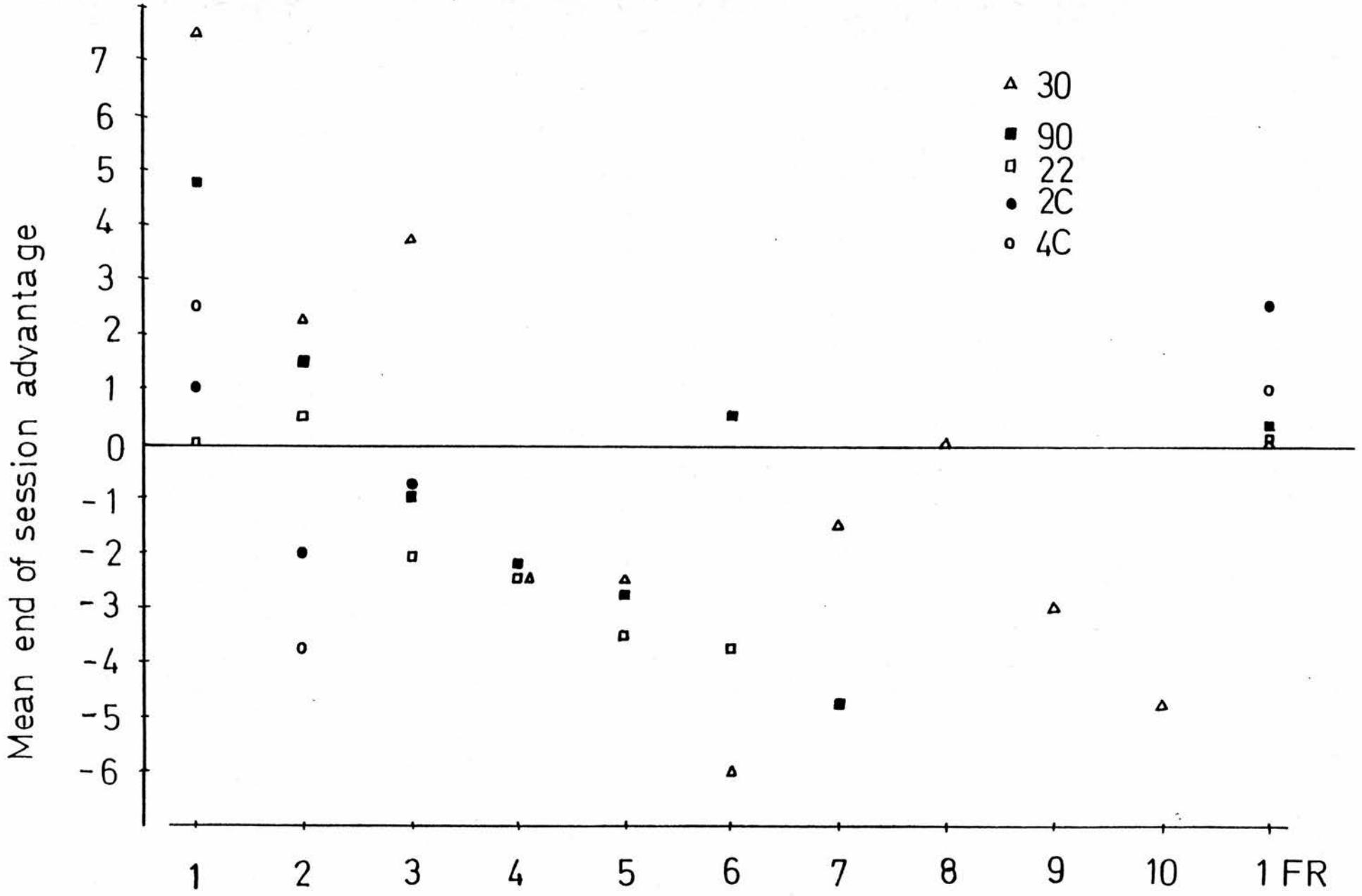

Mean end of session advantage
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
-6
30
90
22
2C
4C
1
2
3
4
5
6
7
8
9
10
1 FR

Figure 94

The mean number of responses (of 4 sessions) produced by a single subject ("30") during successive 5 min. segments of sessions at FR1, FR2 and FR10. Bars represent one standard error.

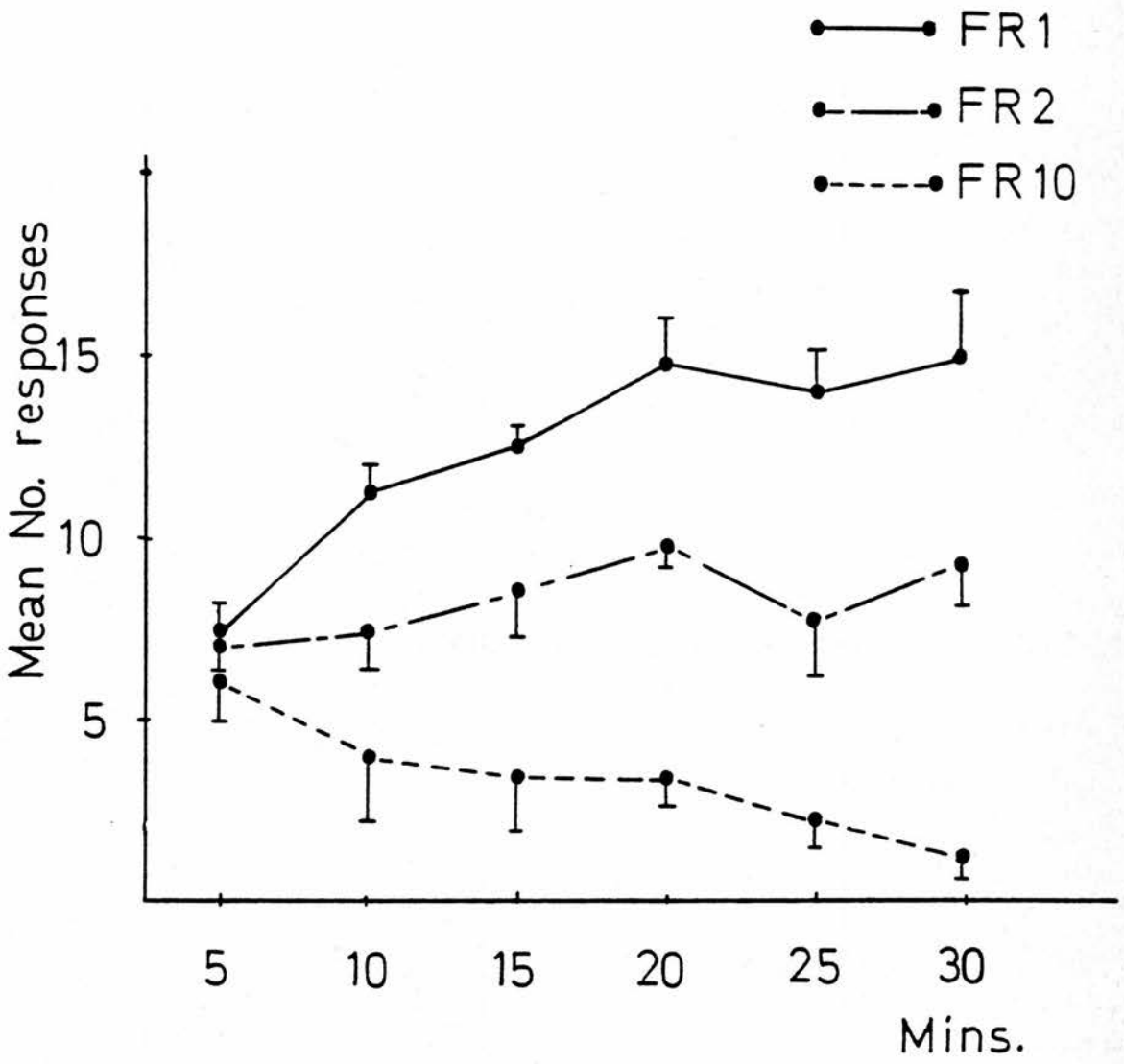

FR1
FR2
FR10
Mean No. responses
15
10
5
5
10
15
20
25
30
Mins.

Table 36

Comparisons of the numbers of rewards in sessions immediately preceding extinction for each time out (T.O.) group.

Significance testing is by Friedman 2-way analysis of variance.

Experimental group

T.O.(mins.)	0	30	60
$\bar{X}$	43.00	55.67	44.17
SEM	9.36	13.02	8.72

Chi = 1.13
k = 3, N = 6
p > .57

Comparison of the total number of responses in training before each extinction condition for the three time-out (T.O.) conditions.

Significance testing by Friedman 2-way analysis of variance.

Experimental group

T.O.(mins.)	0	30	60
$\bar{X}$	650.17	754.5	692.5
SEM	137.54	181.75	132.73
Total Ranks	12	12	12

Chi = 000
k = 3, N = 6
p = 1.00

$\omega = 0$

$L = 72, p > .05$

Table 37

Correlations between the number of responses in extinction and (a) the number of responses and rewards in the pretest
(b) the total number of rewarded responses before extinction.
(c) shows the effect of extinction session serial position on the number of responses in extinction.

(a)

T.O.	Spearman's rho	significance (1-tailed)
all T.O. conditions pooled(N=18)	-.1411	$p > .05$
0(N = 6)	.1429	$p > .05$
30(N = 6)	.6000	$p > .05$

(b)

T.O.	Spearman's rho	significance (1-tailed)
all T.O. conditions pooled(N=18)	-.1652	$p > .05$
0(N = 6)	.4857	$p > .05$
30(N = 6)	.0286	$p > .05$
60(N = 6)	-.0857	$p > .05$

(c)

Extinction serial position	1	2	3	
$\bar{X}$	35.50	28.33	27.50	Chi = .3300
SEM	10.57	5.76	6.07	k = 3 N = 6
Total Ranks	13	12	11	p = .956

CHAPTER 13

13.1 Fixed Ratio Schedules and the Control of Food Intake In the Barbary Dove (Stenopelia risoria)

13.1 (a) Introduction

It has been suggested by Shettleworth (1972, p. 13) that differences between e.g. aggression and food rewards, in their ability to produce increases in operant responding to compensate for increases in FR size, may be due to the homeostatic nature of the feeding system. If homeostatic in this context is taken to mean feeding in response to some deficit, the question of the degree to which undeprived animals show FR compensation can be raised. Roper (1975), using short operant sessions preceded by varying periods of food deprivation, found that the degree of FR compensation shown by mice did increase with increasing deprivation (and decreasing operant reinforcer distance). However, mice did not have to earn all their daily food requirement by operant responding. It may be important that Bolles and Collier (unpublished observation reported in Collier et al., 1972) found that the asymptotic rate of operant responding in rats on an FR10 schedule was higher if they earned all their daily ration in the operant situation rather than part in the situation and part in the home cage. In addition, Roper (1975) fed mice not only standard laboratory chow, but also wheat, a preferred food for mice. This may artificially have increased subjects body weights. This raises the possibility that Roper's findings are an underestimate of the compensatory abilities of the less deprived animals.

The preceding experiments demonstrated that in Betta splendens operant responding for display reward is controlled to a considerable extent by the motivational states induced by reward. The degree to which similar processes may act in the control of food intake must be considered.

In contrast to the early emphasis on depletion-repletion

processes in the control of food intake, some recent studies stress the anticipatory nature of short term feeding (e.g. Collier, Hirsch and Hamlin, 1972; Hirsch and Collier, 1974). The most important sources of evidence for this is the finding of correlations between the size of meals and the intervals of non feeding which follow them (post-prandial correlations; e.g. Thomas and Mayer, 1968; Duncan, Duncan, Hughes and Wood-Gush, 1970; Davies, 1977). In contrast, correlations between the size of meals and the preceding intervals of non feeding (pre-prandial correlations), which would indicate feeding in response to deficit, are not found in freely feeding animals. This raises the possibility of differences between experimentally deprived and undeprived animals in the way food intake is controlled. Since many operant studies have investigated post-deprivation feeding and drinking in Barbary doves (Streptopelia risoria) e.g. McFarland, 1965; McFarland and McFarland, 1968; McFarland and Lloyd, 1973), the present study aims to describe the pattern of feeding in these birds when living in the operant situation and subject to no experimental food deprivation.

It has been suggested, (Zeigler, Green and Leher, 1971, citing a personal communication with Collier), that significant post prandial correlations are most often found where animals are required to expend some effort in obtaining food. However, Levitsky (1974) who reports increasing post-prandial correlations with increasing effort in obtaining food (bar press duration), suggests that these may be attributable to the increasing meal size which increasing effort produces. He provides evidence indicating that increasing meal size by another method (diet manipulation) also increases post-prandial correlations. Studies using fixed ratio (FR) reinforcement schedules to manipulate food availability (e.g. Collier et al., 1972, for rats; Hirsch and Collier, 1974, for Guinea pigs) have found meal size changes with increasing ratio requirement but in these experiments young animals were used which failed to gain weight normally as

the study progressed. The meal size changes found were attributed to processes of growth and its arrest at higher fixed ratios. Levitsky's (1974) study raises the possibility that, had adult animals been used an effect on meal size might still have been found. The dependence of anticipatory feeding (post-prandial feeding correlations) on meal size and the possibility that the latter may depend on factors related to food availability (effort) is of considerable interest. Where a reward is a fixed amount of food and the effort required to obtain it is increased, the way the animal organizes its work in time cannot change the amount of work it must do to earn its daily requirements. An explanation of meal pattern changes in energetic terms is therefore not possible and the nature of the mechanisms responsible is unclear. It is possible that investigation of the internal structure of meals in terms of the relations between bouts (or indiviual rewards in an operant situation) may provide some clues about the mechanisms involved. The present experiment therefore explores the effects of increasing fixed ratio reinforcement schedules on FR compensation, on the pattern (meal size frequency) of feeding and on the infrastructure of meals in adult Barbary doves.

13.1 (b) Subjects and Apparatus

Six adult female Barbary doves (Streptopelia risoria) were randomly selected from departmental stock. For the duration of the experiment birds were housed in cages 35 x 35 x 35 cms. with constantly available grit and water. On one side of each cage was mounted a large panel key (8 x8 cms.) acting as operandum. On the same wall and to the left of the key was a food hopper which could be raised to allow the bird access to food (single grain millet). Above the point of access to food was a green panel lamp illuminated when the hopper was raised.

Light/dark cycle (12:12 hour) was reversed with lights going off at 9a.m. Just before lights off birds were serviced (cage cleaning, water, food, grit replenishment and weighing). Cages were arranged so that birds were visually isolated from each other.

Response (key pecks) recording and reinforcement delivery (hopper raised for 7 seconds) were controlled in all six cages simultaneously by a PDP 11/34 computer. The time of occurrence of each response and reinforcement was recorded on magnetic disc.

13.1 (c) Method

After birds were maintained on reversed light cycle for four weeks, they were trained to key peck for food. This was achieved by allowing them feed for several days from hoppers continuously in the "up" position and thereafter by taping a grain of millet to a key) or manually shaping the response for 7 second rewards. Two weeks were allowed for birds to reach a stable level of operant responding and body weight before being subjected to a progressive series of Fixed Ratio (FR) schedules of reinforcement. The sequence of FR schedules was as follows: 1, 5, 10, 20, 40, 80, 160, 10. The return to FR10 at the end of the experiment acted as a control condition for changes not due to reinforcement schedule. At each ratio data was collected until seven consecutive days of stable response and body weight occurred (less than ± 20% previous day and no perceptible trend).

13.2 Reinforcement Schedule and Bodyweight

13.2 (a) Results

One of the six birds was subjected to persistent apparatus failure and data from it was discarded. Fig. 95

shows that birds maintained their body weights over the range of FR schedules used (Fried., $p>.05$). However, four birds gained weight on the transition from FR160 to FR10, and all birds weighed more during the second period of FR10 than during the first.

Fig. 96 shows that as FR size was increased there was an increase in daily response output. This increase was not however sufficient to maintain a constant rate of reward earnings, (Fig. 97), and these decline with increasing ratio requirement (Fried., $p<.001$). The maintenance of a constant body weight was therefore achieved partly by increasing operant response output and partly by other means, probably an increase in the amount of food ingested per reinforcement.

13.2 (b) Discussion

Other studies indicate that animals may be reluctant to respond to environmental challenge by operant responding where other adaptations are possible. Rats, (Collier, Hirsch and Hamlin, 1972) and cats (Kanarek, 1975), if given control over reward duration, will increase reinforcement size rather than operant response output, as FR size is increased. If no control over reward duration is allowed, some animals will respond by increasing their food utilization efficiency (e.g. rats; Hirsch and Collier, 1974; and Guinea pigs, Collier et al., 1972). These considerations support the view that the course of operant responding for any reward may reflect only part of an animal's adaptive strategy. Differences in operant performance between species and between motivational systems, may to some extent reflect differences in the efficacy and number of alternative and additional adaptive mechanisms available (c.f. Lea and Roper, 1977). Investigation of the relations between adaptive mechanisms (e.g. operant responding and resource conservation) may be important for understanding the different properties of

reinforcers, and the performance differences between species (see Hogan and Roper, 1978, for review).

On the basis of the present results it cannot be said that undeprived birds do show full FR compensation for food reward since an increase in feeding efficiency occurred along with increase in operant response output. Whether full FR compensation would be shown if a fixed amount of food was presented per reward is a question requiring investigation.

13.3 The Patterning of Food Intake and FR Size

Since the body weights of birds in the present study remained stable to FR160 the effect of work requirement on meal patterning can be assessed without the confounding effects of weight change. As in any study concerned with aggregation of events the problem of defining a meal arises. In operant studies rewards are discrete events and in studies of free feeding short breaks occur between feeding bouts. The decision as to whether a reinforcement or a feeding bout is within the preceding meal or begins the following meal demands the use of a criterion interbout or inter-reinforcement interval. The problem then is one of deciding whether an interfeeding interval is small enough to be considered within a meal or sufficiently large to be an inter-meal interval.

Some authors (e.g. Hirsch and Collier, 1974; Collier et al., 1972; Davies, 1977) have used arbitrary criteria for the definition of inter-meal intervals, e.g.

> "a tunnel entrance during which no less than 0.1g food was consumed and where at least 15min.of no further tunnel entrances occurred"
>
> (Levitsky, 1974).

Kissileff(1970) has drawn attention to the wide range of criteria which have been used and has shown how the choice

of criterion can markedly affect the conclusions drawn from a feeding study. He goes on to suggest that a wide range of criteria should be used within studies and only the most robust effects should be admitted. However, if the concept of a meal has any meaning in terms of the behaviour of the animal, attempts should be made to derive an appropriate criterion from the behaviour observed. Several authors have recently used the cumulative log survivorship plot (Cox and Lewis, 1966) to derive criteria for the identification of groups of events (Nelson, 1964; Wiepkema, 1968; Allison and Castellan, 1970; Slater, 1974, 1975; Peterson, 1975, 1976; MacLeod, 1978). This method was used in the present study to derive criterion inter-reinforcement intervals for the definition of meals.

13.3 (a) Method

A cumulative Logarithmic Survivorship Plot was generated for each bird at each ratio in the following way. An interval was considered which is greater than the longest inter-reinforcement interval actually occurring. This interval was broken down into a number of equal parts (ranges) and the frequency of occurrence of intervals less than or equal to the upper limit of each range is computed. The natural logarithm of these cumulative frequencies was then plotted against interval length. The slope of the plot so constructed provides an estimate of the probability of an inter-reinforcement interval "surviving from one range of values to the next. This is interpreted as giving the probability of a reinforcement occurring at any time since the last reinforcement.

Because the birds fed in meals, the plots generated were concave. Fig. 98 shows a plot for a single animal at FR20. The interval to point A represents the minimum inter-reinforcement interval (IRI) occurring. This approximates to the time it takes the bird to perform the run of responses demanded by

the FR schedule. The interval to point B represents the interval likely to be soon followed by feeding. Intervals greater than B are likely to be much longer before another reward is earned. The two segments of the curve on either size of point B therefore represent two differing populations of IRI's, the IRI's above B likely to be within meals, the ones below B, between meals. The interval up to point B was therefore used as the criterion inter-meal interval for that bird at that ratio.

Since in some cases (particularly at higher ratios) there was a range of intervals at which point B could be placed it was always placed where the most horizontal (i.e. right hand) segment of the curve first deviated markedly from the horizontal. This procedure was performed blind with respect to bird and fixed ratio.

13.3(b) Results

Fig. 99 shows that meal frequency decreased nonsignificantly from FR1 to FR10 (Fried., $p>.05$) and increased significantly thereafter (Fried., $p<.01$) to reach an asymptote at FR40. The change in meal frequency over all ratios was significant ($p<.01$). Meal size as a proportion of the number of reinforcements occurring (fig. 100), showed a complimentary effect increasing nonsignificantly from FR1 to FR10 ($p>.05$) and decreasing from FR10 (Fried., $p<.01$) to an asymptote at FR80. The change in meal size over all ratios was significant ($p<.01$).

13.3 (c) Discussion

A comparable experiment by Hirsch and Collier (1974) with Guinea pigs found no systematic change in meal frequency with increases in FR size from FR1 to FR80. Meal size, however, was an inverted u-shaped function of the ratio requirement as in the present study. This finding is interpreted in terms of the occurrence at low ratios of the

increase in meal size normally associated with growth in Guinea pigs (Hirsch, 1973). The decrease in meal size at high ratios is considered due to the failure of animals to maintain their food intake and body weights at control levels. The finding by Collier et al. (1972) that meal size in rats increases and then decreases with increasing ratio requirement may be explained in a similar manner. The rats used were young (50 days at start of experiment) and by FR80 food intake and body weight declined instead of increasing as in control animals.

In the present study, where adult animals were used and no significant body weight changes occurred, increasing fixed ratio requirment still resulted im meal size changes. These changes differ from those reported by Levitsky (1974) using bar press duration changes to decrease food availability. In the present study an initial increase in meal size was followed by a decrease at higher fixed ratios, whereas Levitsky found only meal size increases with increases on required bar press duration. Comments by Thach (1970) reporting a study of fixed ratio effects on primates responding for food and water, indicate a breakdown in meal structure with increasing FR size but no data analysis was carried out to support the statement. Before attempting an explanation of the results of the present study the nature of the system controlling meal taking will be considered further.

13.4 (a) Feeding Pattern Correlations

Collier et al., (1976) have pointed out that the pattern of meal taking in most free feeding animals is such that in the short term, energetic deficit is unlikely to occur. In support of this, Collier et al., (1972) report that investigations of the stomach contents of freely feeding rats and Guinea pigs never revealed a completely empty stomach. In the Barbary dove, even the nocturnal period of non-feeding is

likely to be attenuated in its effects by the availability of food stored in the crop during mid-afternoon (MacLeod, 1978).

As mentioned earlier, if inter-meal deprivation did control the size of the following meal then positive pre-prandial correlations would be expected (le Magnen and Tallon, 1966), but such correlations have not been found in normal undeprived animals. In contrast to this, significant post-prandial correlations have been reported by many authors (e.g. Balagura and Coscina, 1968, 1969; Balagura and Davenport, 1970; le Magnen and Devos, 1970; la Rue and le Magnen, 1972; Levitsky, 1974; Slater, 1974; Peterson, 1975). Such correlations have been taken to indicate that meal initiation may be inhibited by the effects of the previous meal. However, such correlations are not always obtained (e.g. Levitsky and Collier, 1968; Collier et al., 1972; Premack and Kintsch, 1970; Zeigler, Green and Lehrer. 1971; Panksepp, 1973; Kenney and Mook, 1974; MacLeod, 1978), and it has been suggested (Panksepp, 1973) that in some studies where significant post-prandial correlations have been found they may be attributable to the use of illegitimate statistical procedures. In addition, Hirsch and Collier (1974) have suggested that the pooling of data across animals for the computation of correlations (as in e.g. le Magnen and Devos, 1970) might spuriously inflate the correlations obtained. Neverthless, studies using appropriate statistical procedures and which did not pool data have produced significant post-prandial correlations (e.g. Thomas and Mayer, 1968; Duncan Duncan, Hughes and Wood-Gush,1970).

An additional factor which may operate in the production of significant post-prandial correlations is meal size. Levitsky (1974) cites evidence that a minimum meal size may be necessary for post-prandial correlations to occur and provides evidence suggesting that work requirement may produce significant correlations by increasing meal size. This would lead to the expectation in the present study that significant post-prandial correlations would increase

from FR1 to FR10, where meal size is at its greatest, and decrease thereafter. Data from the present study was therefore analyzed to produce post- and pre-prandial correlations for each bird at each ratio requirement. No pooling of data was performed.

13.4 (b) Results and Discussion

Table 38 shows the significances of post-prandial and pre-prandial correlations computed for each animal at each ratio. Post prandial correlations were most marked at FR5 and FR10 and decreased from FR10 to FR160. The correlation was therefore most evident where feeding was most bouted (see Fig. 100), with all five birds showing significant post-prandial correlations at FR5 and FR10. In contrast the pre-prandial correlations were much less marked at all ratios, but peaked at FR40 with three out of five birds showing a significant correlation. It cannot be said therefore that the diminuation in anticipatory feeding as FR size increased was accompanied by an increase in restorative feeding. Interestingly, Levitsky (1970) reports a sharp rise in pre-prandial correlations (3 of 3 rats significant) at bar press durations of 15secs. (the range used was 1 - 50 secs.), and declining thereafter.

Shettleworth's (1972) suggestion that FR compensation may be a property of homeostatic systems is not supported by the findings of significant post-prandial correlations and the virtual absence of significant pre-prandial correlations. These indicate that at no ratio size, with the possible exception of FR40, are birds responding to inter-meal deficit, and at low FR sizes thay are feeding in advance of their energetic needs. Interesting in this context, MacLeod (1978) found that Barbary doves will learn to anticipate a

period of deprivation if appropriate cues are given, pre-empting deficit by anticipatory overeating.

13.5 The Structure of Meals

Wiepkema (1971) in an observational study of free feeding mice found that the bouts of continuous feeding of which meals are composed, progressively lengthened over the initial stages of the meal. Using automatic recording tecniques, Peterson (1975, 1976) with mice and MacLeod (1978) with Barbary doves, found similar effects. Wiepkema argued that if the periods of uninterrupted feeding are used as an index of the animal's feeding tendency, then as the meal progressed net feeding tendency is increasing rather than decreasing. Furthermore since there was no tendency for the inter-bout intervals to decrease, this change was in persistance in feeding, i.e. the probability of bout cessation, rather than in the probability of initiating feeding. This increase in persistence is attributed to the action of "positive feedback" activated by contact with food. Since Wiepkema found no effect of contact with food on the tendency to initiate a feeding bout, it may be asked whether in the operant situation where a bout (a reinforcement) is arbitrarily terminated, contact with food can motivate the reinitiation of feeding (operant responding).

Landless (1974, 1975) in an operant study of demand feeding in Rainbow trout showed that a single presentation of food at a time when spontaneous feeding was not expected would induce feeding whose characteristics resembled those of normal meals. Similar priming effects have been reported by several authors for a range of species and rewards. In rats a small amount of the reward substance before a session will enhance subsequent performance (for water: Bruce, 1937; for food: Morgan and Fields, 1938). Where an animal has learnedmore than one response for more than one reward, a

free reward will lead to the production of the response appropriate to it (Konorski, 1967, p. 21). In extinction a free presentation of chocolate milk reward in rats will lead to a temporary resumption of operant responding (Ranksepp and Trowill, 1967). De Noble and Caplan (1977) Deluty (1976) and Eiserer (1978) have demonstrated that the presentation of non-contingent food reinforcement in rats produced a short lived elevation in subsequent operant response rate, and many studies report that response rate increases over the first few minutes of a test session ("warm up" e.g. Barbary doves for water: McFarland and McFarland, 1968; rats for food: McCleery, 1977, and Siamese fighting fish for aggression: this thesis ch. 7.4). It seems then that contact with a range of reinforcing stimuli may motivate the performance of operant responses.

Data from the present experiment was further analyzed to determine whether such facilitory processes operate within meals for the undeprived Barbary dove in an operant situation.

13.5 (a) Method

For each bird at FR1 all meals greater than 11 reinforcemnts in size were identified and the mean intervals between successive reinforcements were computed for the first five and last five rewards of each meal.

13.5 (b) Results

Fig. 101 shows a decrease in mean inter-reinforcement intervals over the first stages of the meal (Fried., $p<.01$). The temination of meals was not characterized by a progressive increase in IRI (Fried., $p>.05$). There is evidence then of a facilitation of feeding into the meal but meal termination did not resemble a typical satiation curve. How far these findings can be generalized to include meals of fewer than 11 reinforcements will be considered later.

13.5 (c) Discussion

As well as increasing the lengths of successive feeding bouts in freely feeding animals, i.e. increasing the tendency to continue feeding, (Wiepkema, 1971) contact with food can increase the tendency to reinitiate feeding in undeprived birds by motivating the performance of an operant reponse. The absence of a progressive increase in IRI's at the end of the meal (only the last IRI is longer) agrees with McLeod's (1978) finding that in freely feeding Barbary doves, no gradual shortening of feeding bouts occurs within meals. Instead the last bout of the meal is truncated. The classical satiation curve as described by e.g. Skinner, (1932a, b), Bousfield (1933) and McCleary, (1977) may be a response specific to recovery from periods of food deprivation much longer than those occurring between meals in freely feeding animals. McCleary's (1977) statement that

> "It is a matter of common observation that this (satiation) curve is a negatively accelerated function of time since the start of the meal"

may not therefore be generally applicable.

The facilitatory processes acting during meals may in part determine the size of meals which occur. This implies that the changes in meal size which occurred with changing FR requirement should be accompanied by changes in the intrameal facilitation of feeding.

13.6 Effects of FR Schedule on the Structure of Meals

13.6 (a) Method

For each bird at each fixed ratio, all meals of greater than 11 reinforcemnets were analyzed in terms of the successive intervals between the first five and the last five reinforcements.

13.6 (b) Results and Discussion

Fig. 102 shows the successive mean IRI's at the beginning and end of meals at each ratio and gives the significance levels of the serial order effect. From FR1 to FR10 a significant reduction occurs in mean IRI's over the first five reinforcements (Fried., $p<.01$). Above FR10 facilitation is less evident and non significant. Over the last five reinforcements of the meal, IRI's show some tendency to increase with FR size although this effect is significant only at FR10 ($p<.05$).

It is possible that the failure to find intrameal facilitation in feeding at high ratios is due to the reduction in the number of meals greater than 10 reinforcements as FR size increases. The data were therefore re-analyzed using the first five IRI's of all meals of greater than five rewards. This greatly increases the number of data items available at high ratios (e.g. at FR160, mean number of items increases from 25.2 to 66.6). Fig. 103 shows that the IRI serial order effect for meals of over five rewards is similar to that for meals of over 10 rewards. As FR size increases above FR10 meal size decreases and there is a concomitant decrease in the facilitation of feeding into meals.

At low fixed ratios it was shown that meals size increases. The suggestion that meal size is caused by intra-meal facilitation implies the expectation that from FR1 to FR10, the amount of facilitation occurring would increase. To investigate this, a facilitation index was used to describe the degree of facilitation occurring in a manner allowing direct comparison across fixed ratios.

13.6 (c) Method

An index of facilitation was computed for each fixed ratio size by taking for each bird the mean of the first

inter-reinforcement intervals in meals greater than five rewards and dividing this mean by the mean of the 5th IRI's. This index of intrameal facilitation is comparable across ratios with an index of greater than one indicating a decrease in IRI's into the meal and an index of less than one an increase in IRI's.

13.6 (d) Results

Fig. 104 shows the mean facilitation index for each FR size. It can be seen that the mean value of the facilitation index peaked at FR5, and at FR10 was still greater than at FR1. Thereafter it declined, falling below 1 at FR160. The change in facilitation over fixed ratios (Fried., $p<.001$) parallels the changes which occurred in meal size.

13.6 (e) Discussion

As FR size was increased, meal size first increased and then decreased. Parallel to meal size changes, and possibly caused by them, was an increase and then a decrease in post-prandial feeding correlations. Furthermore, it can be suggested that the changes in meal size observed over fixed ratios may depend on the changing degree of intrameal facilitation in feeding shown in the previous analysis. A question not yet raised concerns the aspect of FR increase which brings about this change in facilitation.

If meals are maintained by positive feedback increasing the animal's tendency to work for further rewards, as seems likely from the facilitation of feeding into meals and its change with meal size, then we must consider the possible effects of FR schedules on such motivational processes. A characteristic of operant situations which is not generally considered to have motivational implications is the discrete nature of reinforcements. The animal performs operant responses, gains access to food and then after an arbitrary

period (7 secs. in this experiment) food is withdrawn and the animal must perform further responses to reinitiate contact. If the tendency to reinitiate feeding (perform further responses) is due in part to the cumulative aftereffects of previous rewards, then a fixed ratio reinforcement schedule may not simply impose a work requirement. Work takes time to perform and it is possible that during this time the motivating effects of the previous reward are decaying.

In many cases in which a behaviour is facilitated over successive contacts with some stimulus (warm up), the aftereffects of contact decline with time since the stimulus was withdrawn. This decay of excitation or positive feedback is often a negative exponential function. Such warm up and decay processes seem to occur in a wide range of motivational systems (e.g. intracranial self stimulation; Deutsch and Howarth, 1963; attack in cichlids: Heiligenberg, 1974; in Siamese fighting fish: Chs. 10.3 and 10.4 of this thesis: operant behaviour for aggression in Siamese fighting fish: ch. 7.3 of this thesis: rats maze running for water: Hunsicker and Reid 1974; maze running for food: Morgan and Fields, 1938; and lever pressing for food: Deluty 1976).

Deluty's (1976) study is of some importance in this context. Food deprived rats bar pressing on a random interval (1 min.) reinforcement schedule were presented with free (non-contingent) food pellets. The effect of free reinforcers was to increase the subsequent rate of operant responding above its mean level. Rasponse rate declined to baseline approximating to a negative exponential function of time since the free reinforcer (half-life of 5-10 secs.). If a similar process is associated with reinforcement in the present study, then we must consider the possibility that positive feedback decay occurs while the animal is earning the next reward. As the ratio requirement increases so does the minimum interval which can occur between rewards.

Fig. 105 shows the change in minimum IRI with increasing ratio requirement as derived from the cumulative logarithmic survivorship plots for individual birds at each ratio. It can be hypothesised that the change in meal pattern observed with increasing ratio requirement and the decrease in intrameal facilitation are due to the increasing "length of a 'time out' period" (the time it takes to perform the number of responses required by the ratio) rather than the number of responses required per se.

Because of the large minimum IRI's at high fixed ratios, birds maybe less motivated by previous rewards to continue meals, meal termination is earlier than it would otherwise be and the animal regulates food intake successfully by reinitiating feeding sooner (increasing meal frequency). Since the decline in meal size was not accompanied by increasing pre-prandial feeding correaltion, this reinitiation may not be in response to deficit accumulated since the last meal. Instead meal initiation, inhibited at low ratios by large preceding meals (significant post prandial correlations) may fail to be inhibited by smaller meals at high ratios. As mentioned earlier, Levitsky (1974) cites evidence suggesting that a minimum meal size in calories may be necessary for such inhibition to occur.

The question of exactly which environmental variables are operating to produce the meal size changes reported here can only be answered by an experiment separating the variables of time and work. This would indicate whether the increase in meal size from FR1 to FR10 was caused by the same environmental varible as caused the decrease in meal size from FR10 to FR160. In any case it seems a possibility that whatever the envornmental factors are, they are operating on a single aspect of the feeding control system, the processes controlling intrameal facilitation in feeding.

Why initial increase in meal size (from FR1 - FR10) should occur is more difficult to account for. One possibility is that it may be related to findings that instrumental responding after the withholding of an expected reward increases in vigour (the "frustration effect", e.g. Levy and Seward, 1969). This may be caused by excitation which continues to increase for a time after reward termination, as in Betta splendens attack (ch. 10.3). Another possibility concerns any effect of the rateof ingestion of food on the strength of post-reward positive feedbacks. As pointed out earlier, increasing their rate of operant responding was not the only means whereby birds maintained a constant food input with increasing fixed ratio size. The amount of food ingested per reward probably increased in addition to the increased rate of responding. How such increases in reinforcement size would affect intrameal facilitation and meal size in undeprived Barbary doves is not clear but a study by McFarland and Lloyd (1973) suggests that such increases might be important. Deprived Barbary doves in an operant situation where both food and water could be earned, did not randomly alternate between alternative behaviours. Instead they "locked on" to one behaviour (e.g. feeding) persisting in this activity for some time before switching to the other. Several such alternations occurred in test sessions and the degree to which an animal persisted in one behaviour before changing to the other was described by a "lock on index". This index has a maximum value of 1 if the bird takes all of its requirments of one comodity before engaging in the alternative activity. Increasing a "time out" imposed after each reward decreases the lock on index. Furthermore, it was not rate of reward earning per se which determined locking on, but the rate of ingestion of the reward substance. Increasing reward size along with time out duration,to hold rate of ingestion constant,resulted in a constant "lock on" index. In addition,

it was shown that locking on was not affected by work requirement (see McFarland 1971, p. 247). Although these studies used deprived animals, it is nevertheless appropriate to consider the possible implications of such processes in the present experiment.

As the minimum inter-reinforcement interval (IRI) increased with FR schedule the maximum reinforcement rate decreased (Fig. 106). In McFarland and Lloyd's experiment increasing time out duration decreased "locking on". If similar processes were operating in this experiment meal size would be expected to decrease over FR schedules as actually occurred from FR10 to FR160. However, locking on is determined by the rate of ingestion of the reward substance and increasing FR schedule was accompanied by an increase in the amount of food ingested per reinforcement. Fig. 107 shows the relative value of a reward at each fixed ratio in terms of its value at FR1, based on the assumption that constant body weight implies a constant food intake. These values can be used to correct the maximum reward rate and provide an estimate of the maximum rate of food intake at each fixed ratio (Fig. 108). The relation between the maximum rate of food intake at each ratio (as estimated) and fixed ratio size resembles the relations between meal size and fixed ratio schedule more closely than does the relation between fixed ratio and maximum reward-rate. However, since maximum rate of food intake does not increase from FR1 to FR5, this cannot account completely for the effects of FR schedule on intrameal facilitation and meal size.

The results of this investigation of food rewarded operant performance suggest that constraints on the rate of food intake imposed by the operant situation, and by reinforcement schedules, may interact with particular aspects of the food intake control system, in this case the positive feedback decay process and possibly the tendency to increase feeding efficiency during rewards. Again, it must be pointed out that until an experiment is carried out which separates the two variables of work and "time-out", the explanations advanced here remain tentative hypotheses.

The question originally posed concerned the degree to which FR compensation would be shown by undeprived animals living in the operant situation, and the mechanisms which produce this compensation when it occurs. It was found that birds did in fact show FR compensation, but that body weight was not maintained by this response alone. In addition to increasing the daily rate of operant responding, birds increased their feeding efficiency. Whether full FR compensation would occur if a fixed quantity of food were delivered at each reinforcement is a question which remains to be answered. For this reason, and since Roper's (1975) experiment with food reward in mice used short operant sessions and involved the maintenance of animals partly on a preferred diet, comparison with Roper's results is difficult. It can be said, however, that whereas experiments involving deprivation procedures may produce full FR compensation for fixed quantities of reward, in undeprived Barbary doves no evidence was found to support the hypothesis that FR compensation was produced by naturally occurring inter-meal deprivation.

Figure 95

Mean body weight of birds as a function of fixed ratio size. Bars represent two standard errors. Significance testing was by Friedman 2-way analysis of variance. N = 5.

	1	5	10	20	40	80	160	10
$\bar{X}$	162.1	159.6	158.2	158.6	162.1	161.2	160.8	173.5
SEM	4.53	5.22	6.40	6.45	7.13	8.91	14.60	6.20
Total Ranks	24	18	17	15.5	26	20.5	20.0	39

Chi = 13.25
df = 7
$p > .05$

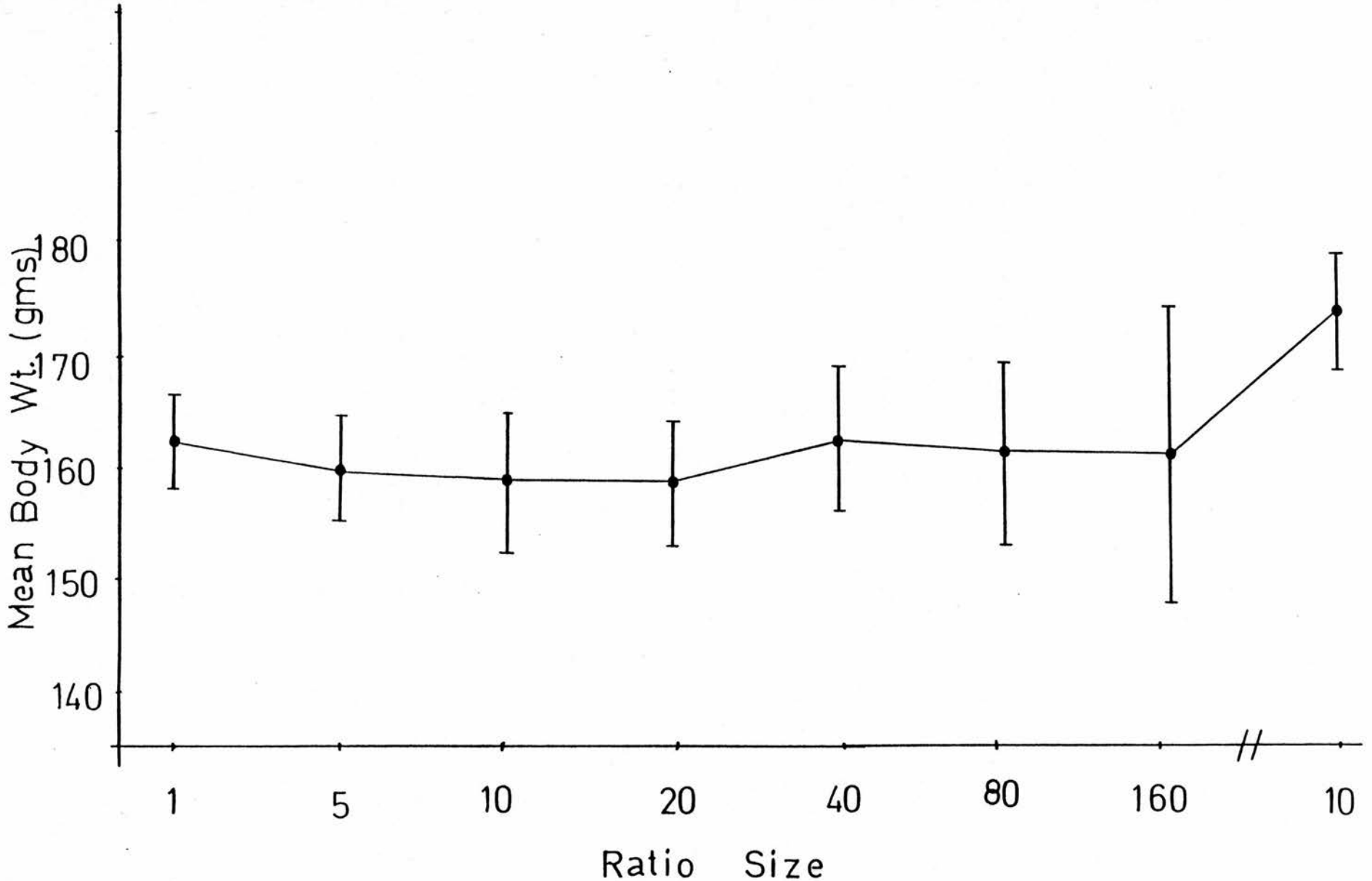

Mean Body Wt. (gms)
180
170
160
150
140
1
5
10
20
40
80
160
10
Ratio Size

Figure 96

Mean number of responses emitted per day as a function of fixed ratio size.

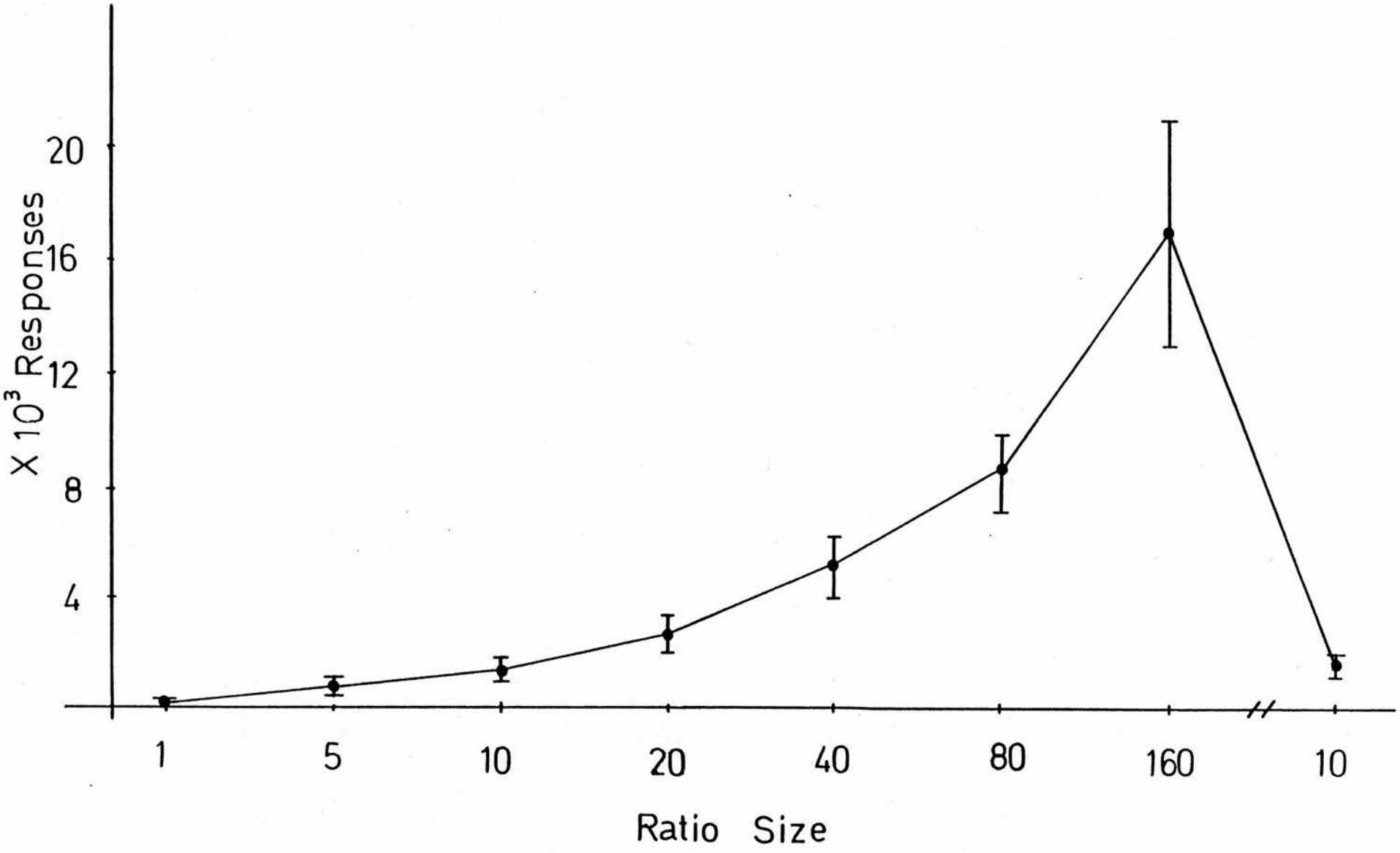

X 10³ Responses
20
16
12
8
4
1
5
10
20
40
80
160
10
Ratio Size

Figure 97

Mean number of reinforcements earned each day as a function of fixed ratio size. Bars indicate two standard errors. The significance of the change from FR1 to 160 was tested by Friedman 2-way analysis of variance.

$$\text{Chi} = 23.31$$
$$df = 6, \quad N = 5$$
$$p < .001$$

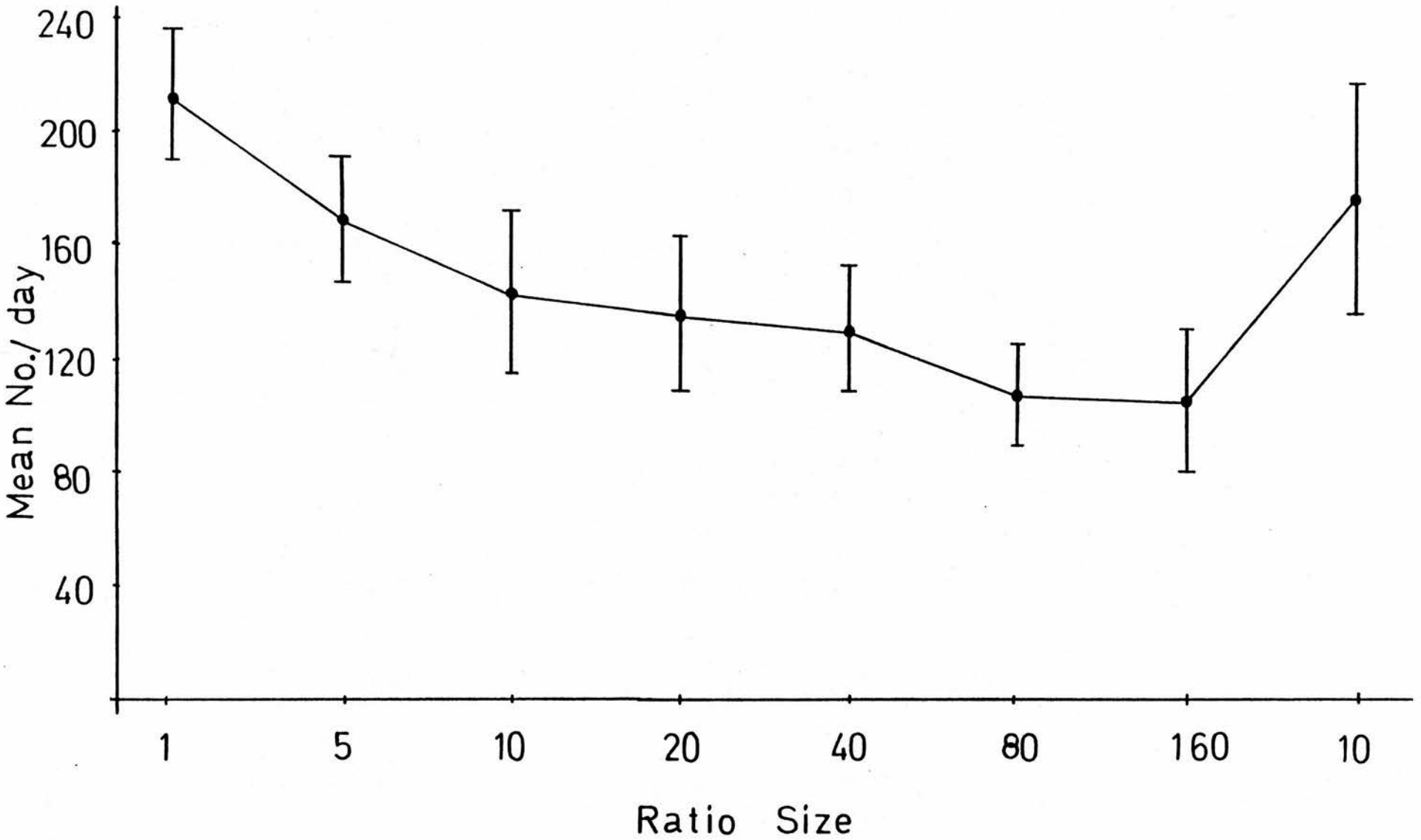

240
200
160
120
80
40
Mean No./ day
1
5
10
20
40
80
160
10
Ratio Size

Figure 98

Example logarithmic survivorship plot for an individual bird at FR20. A indicates the minimum inter-reinforcement interval (IRI). B indicates the criterion IRI above which intervals are inter-meal intervals.

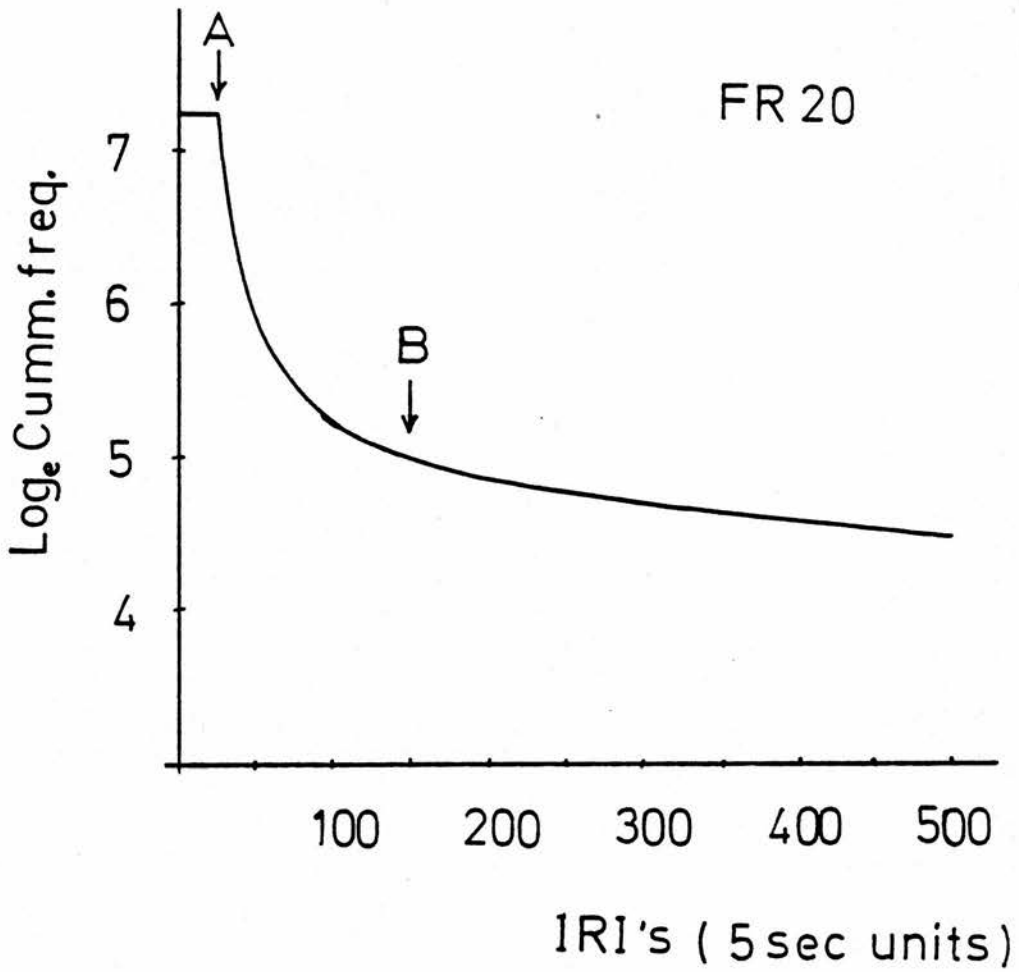

A
B
FR 20
7
6
5
4
Log$_e$ Cumm. freq.
100
200
300
400
500
IRI's (5 sec units)

Figure 99

Mean frequency of meal taking as a function of fixed ratio size. Bars indicate two standard errors.

The significance of the change in mean frequency with ratio size was tested by Friedman 2-way analysis of variance.

	Chi	Significance
All ratios(1 - 160)	18.34	$p < .01$
1 to 10	5.20	N.S.
10 to 160	16.16	$p < .01$

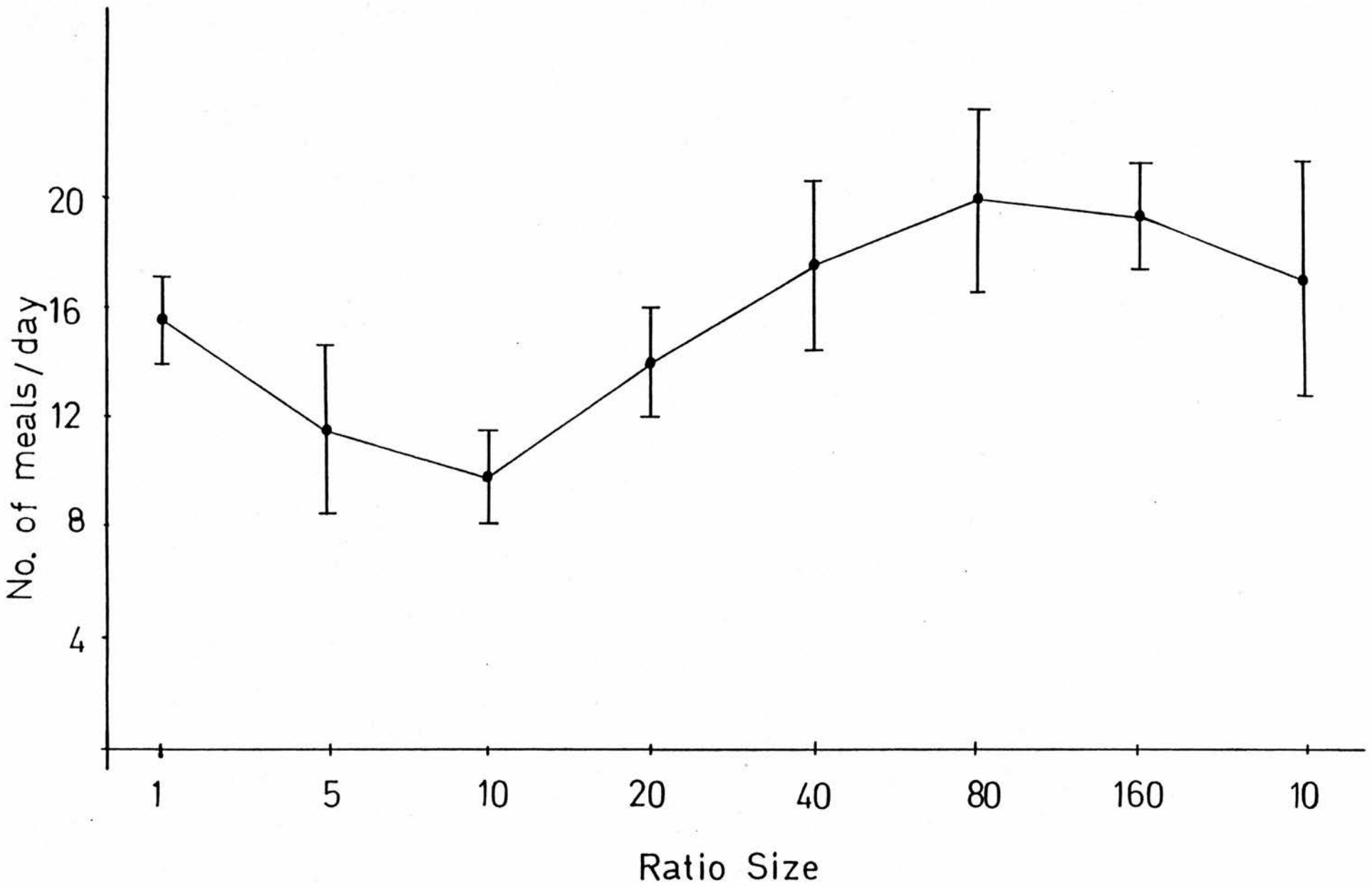

No. of meals / day
20
16
12
8
4
1
5
10
20
40
80
160
10
Ratio Size

Figure 100

Mean meal size (as a percentage of the daily number of reinforcements) as a function of fixed ratio size. Bars indicate two standard errors.

The significance of the change in meal size with ratio size was tested by Friedman analysis of variance.

	Chi	Significance
All ratios(1-160)	17.57	$p < .01$
1 to 10	5.20	N.S.
10 to 160	16.16	$p < .01$

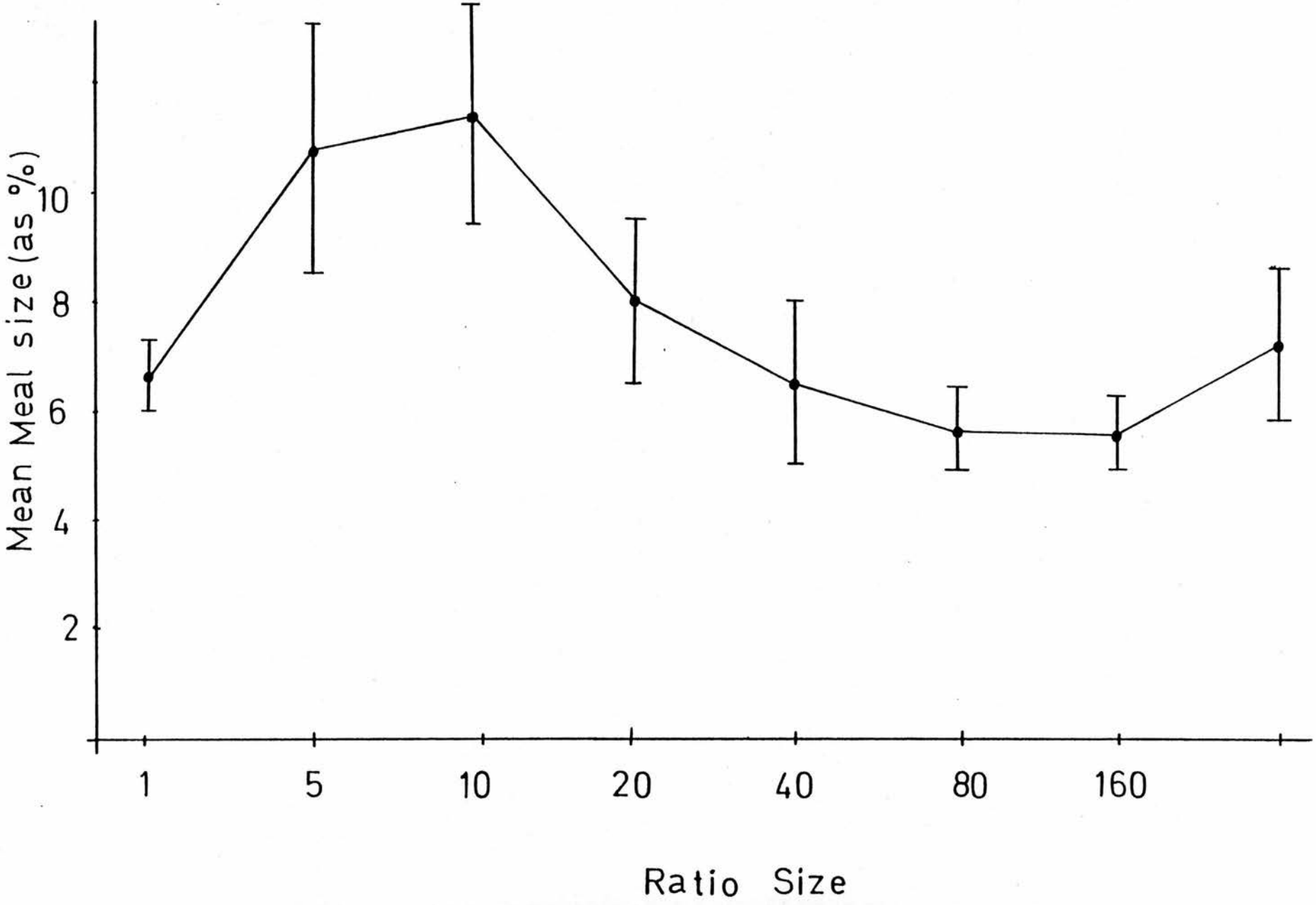

Mean Meal size (as %)
10
8
6
4
2
1
5
10
20
40
80
160
Ratio Size

Figure 101

Grand means of the means for each bird, of the first 5 and last 5 inter-response intervals (IRI) in all meals of greater than 10 reinforcements recorded at fixed ratio of 1. Bars indicate two standard errors.

The significance of the change in IRI with serial position in the meal was tested by Friedman 2-way analysis of variance.

	Chi	Significance
First 5	13.92	$p < .01$
Last 5	7.55	N.S.

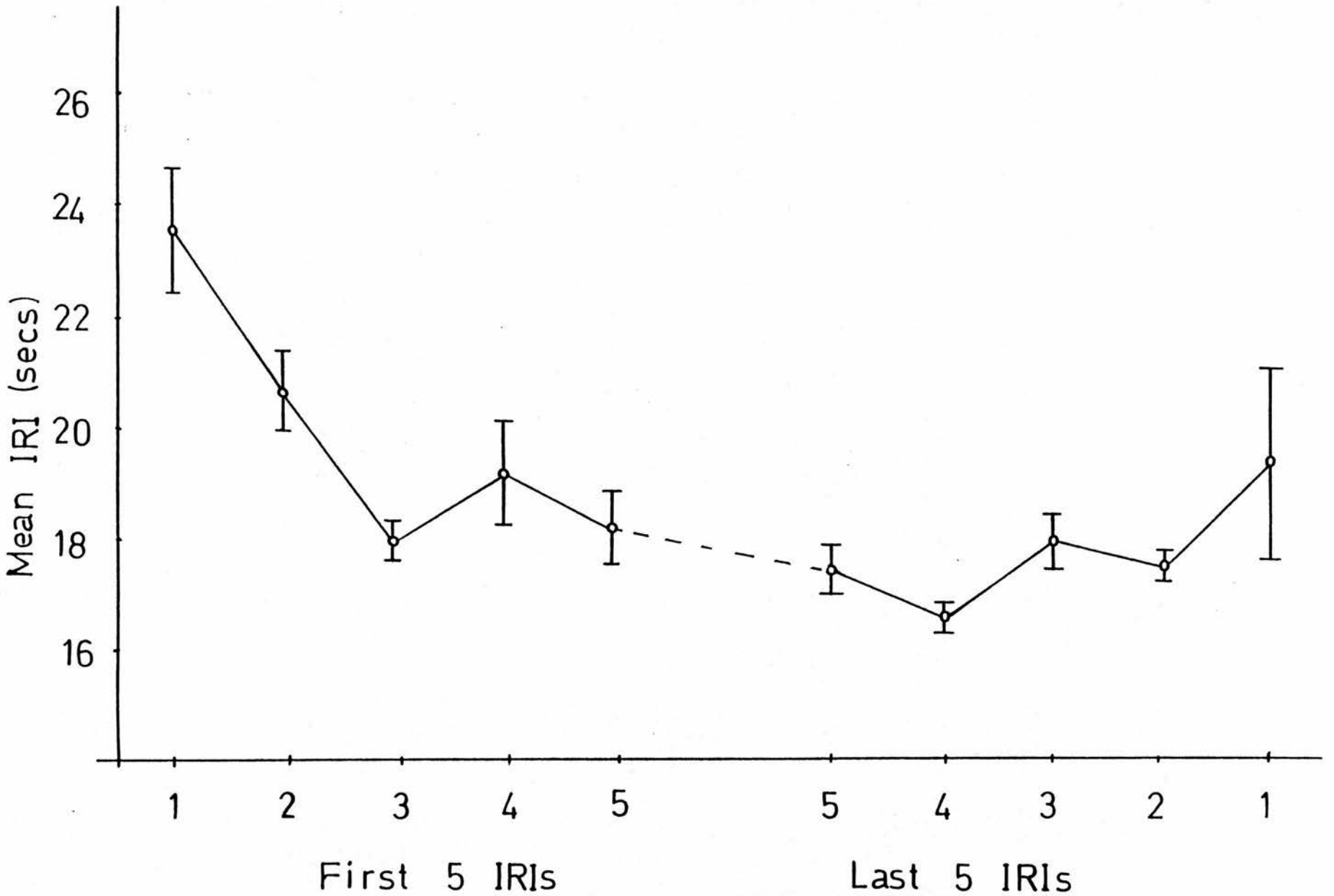

Mean IRI (secs)
26
24
22
20
18
16
1
2
3
4
5
5
4
3
2
1
First 5 IRIs
Last 5 IRIs

Figure 102

Inter-reinforcement interval (IRI) serial order effect at each fixed ratio size. Significance testing was by Friedman 2-way analysis of variance.

Fixed Ratio Size	First 5 Chi (significance)	Last 5 Chi (significance)
1	13.92 ($p < .01$)	7.55 (N.S.)
5	16.16 ($p < .01$)	7.88 (N.S.)
10	13.6 ($p < .01$)	10.88 ($p < .05$)
20	6.56 (N.S.)	7.04 (N.S.)
40	8.32 (N.S.)	2.88 (N.S.)
80	14.72 ($p < .01$)	4.32 (N.S.)
160	4.64 (N.S.)	7.20 (N.S.)

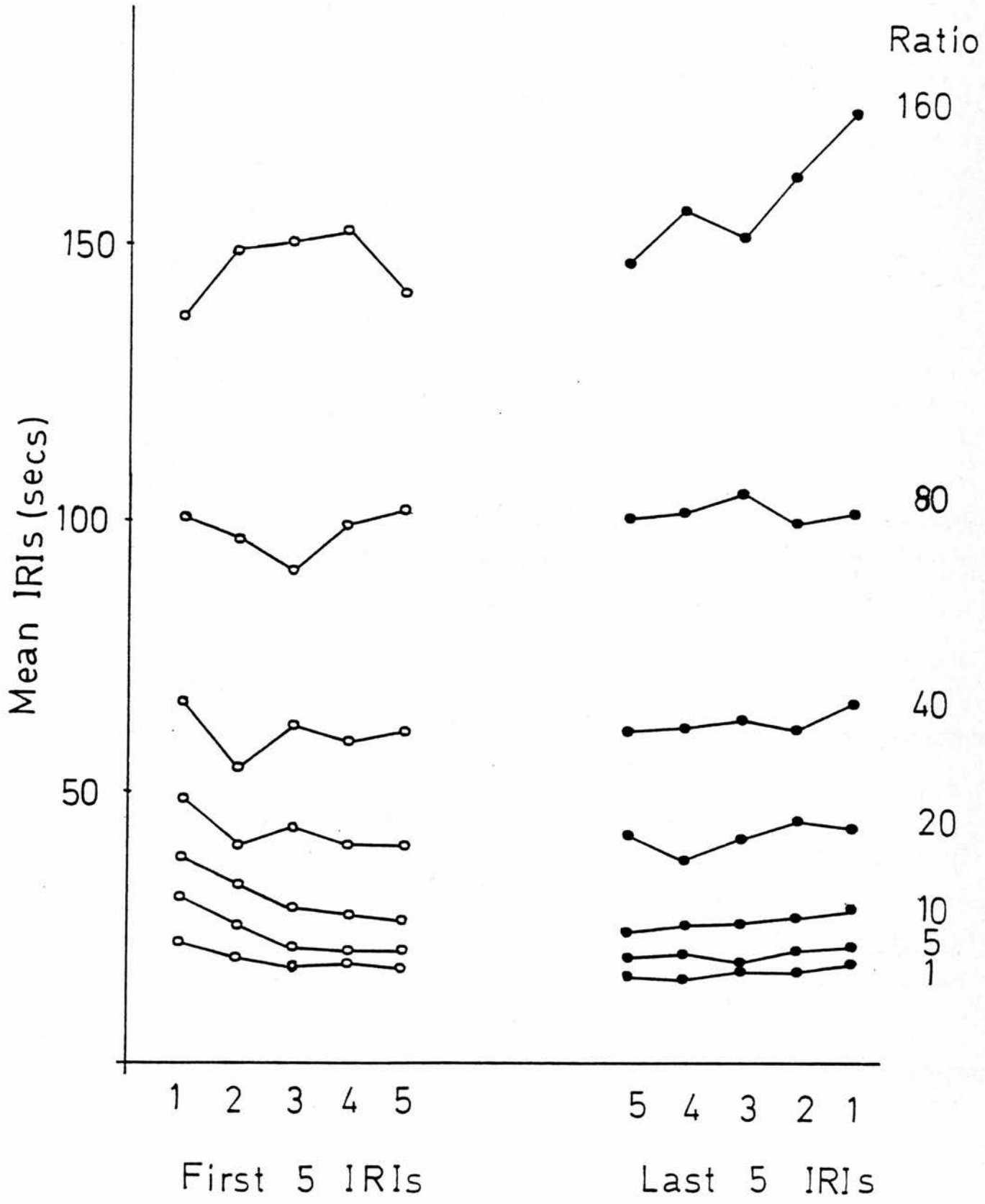

Ratio
160
80
40
20
10
5
1
150
100
50
Mean IRIs (secs)
1 2 3 4 5
5 4 3 2 1
First 5 IRIs
Last 5 IRIs

Figure 103

Inter-reinforcement interval (IRI) serial order effect at each ratio size for all meals of greater than 5 reinforcements. Significance testing was by Friedman analysis of variance.

Fixed Ratio Size	Chi	Significance
1	12.32	$p < .02$
5	16.28	$p < .01$
10	13.05	$p < .02$
20	10.40	$p < .05$
40	10.24	$p < .05$
80	8.80	N.S.
160	7.84	N.S.

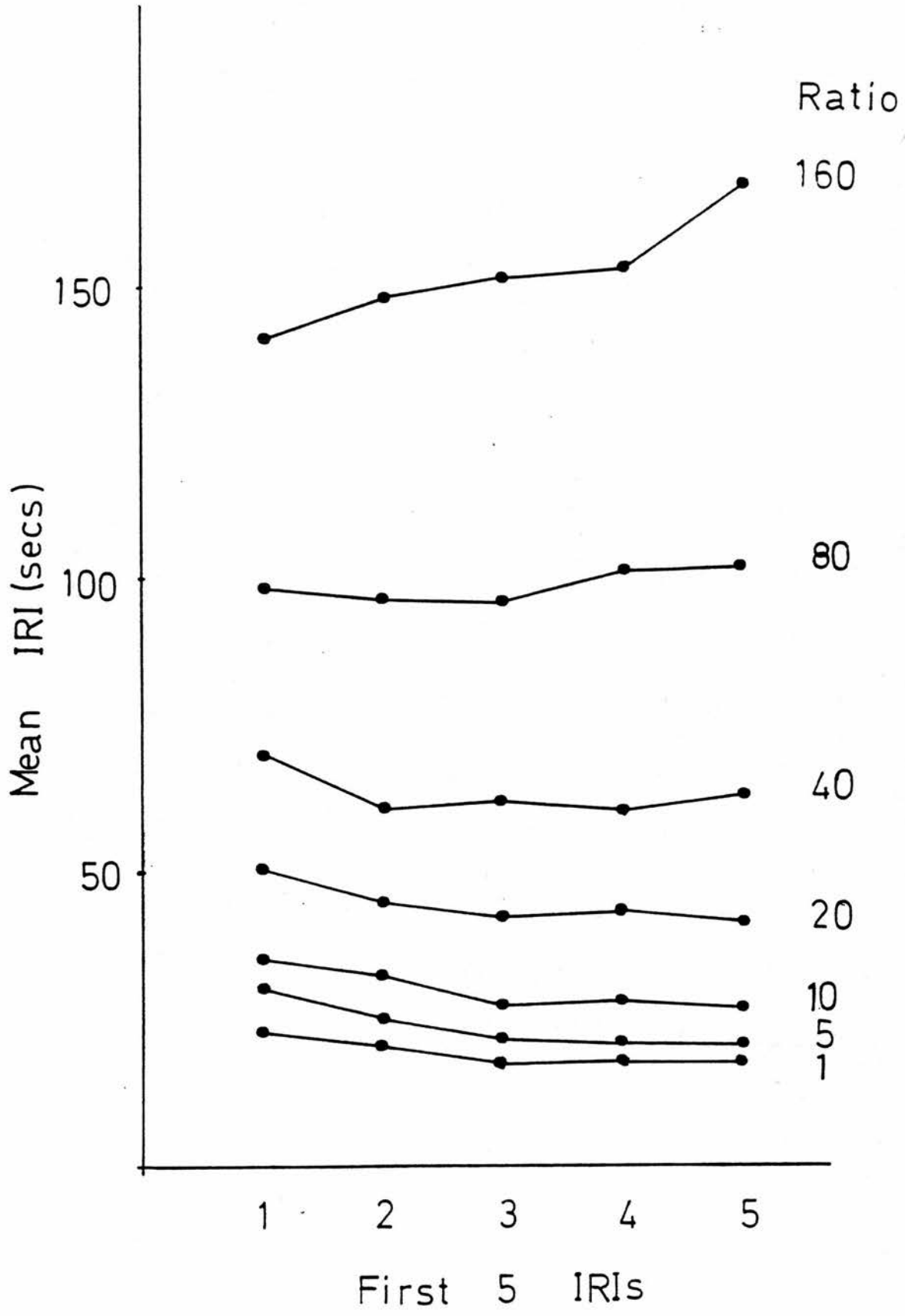

Ratio
160
80
40
20
10
5
1
150
100
50
Mean IRI (secs)
1
2
3
4
5
First 5 IRIs

Figure 104

Mean intra-meal facilitation index (mean first IRI divided by mean last IPI) for meals greater than 5 rewards, as a function of ratio size. Bars indicate two standard errors. Significance testing by Friedman 2-way analysis of variance.

$$\text{Chi} = 24.60$$

$$df = 7$$

$$p < .001$$

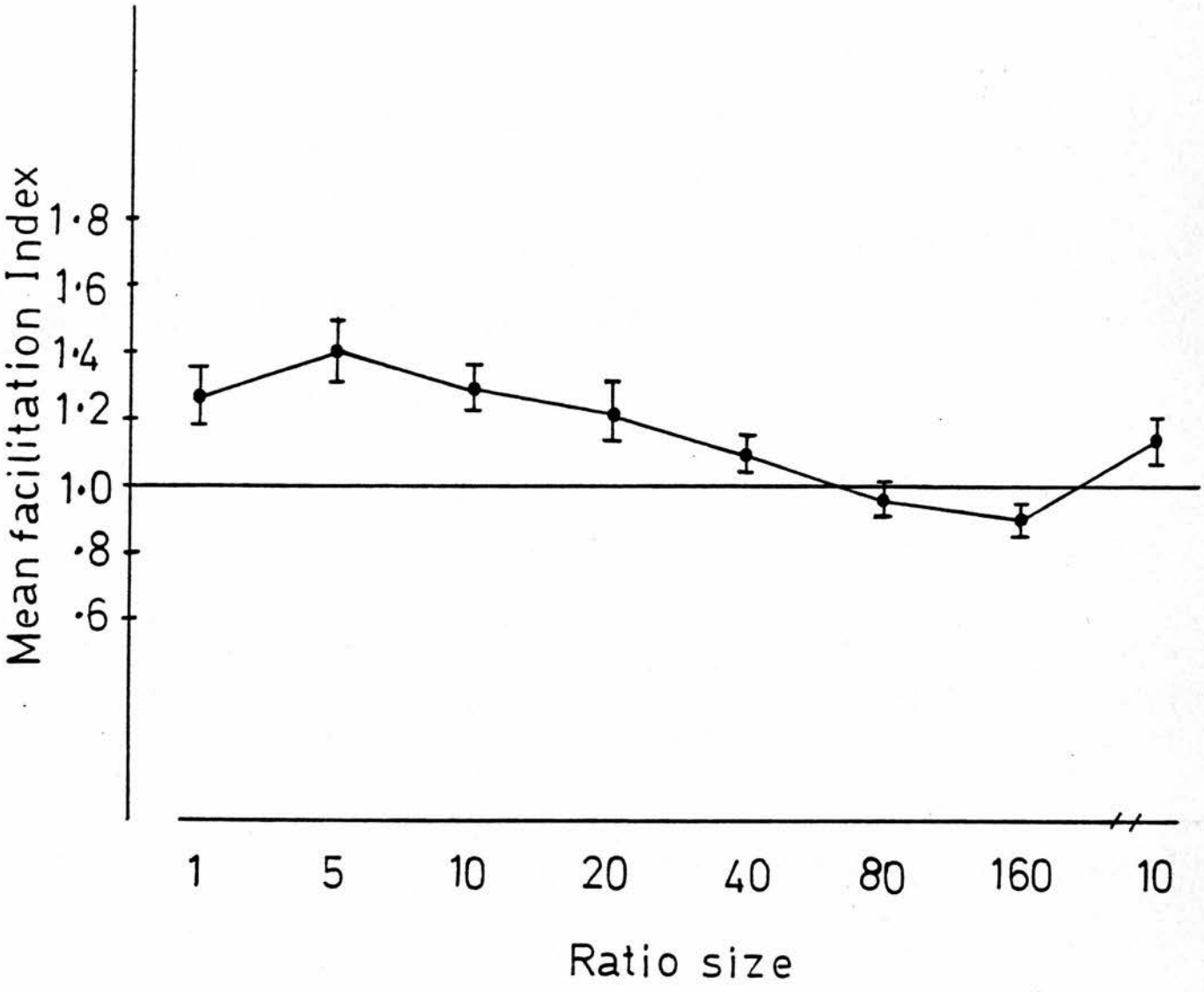

Mean facilitation Index
1·8
1·6
1·4
1·2
1·0
·8
·6
1
5
10
20
40
80
160
10
Ratio size

Figure 105

Mean minimum inter-reinforcement interval (IRI) as a function of fixed ratio size. Bars indicate two standard errors. The horizontal line at 7 seconds indicates the duration of reinforcement for comparison.

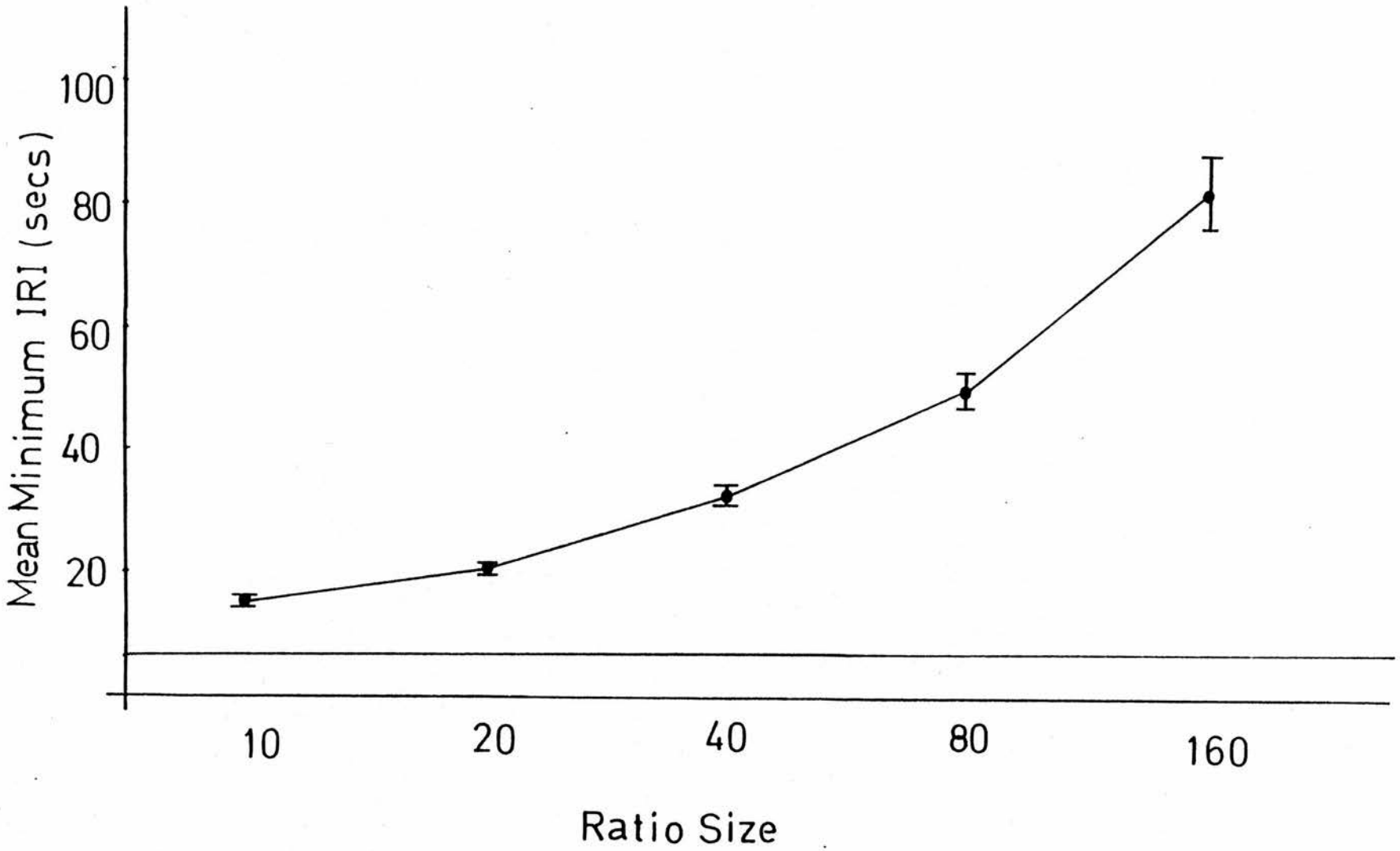
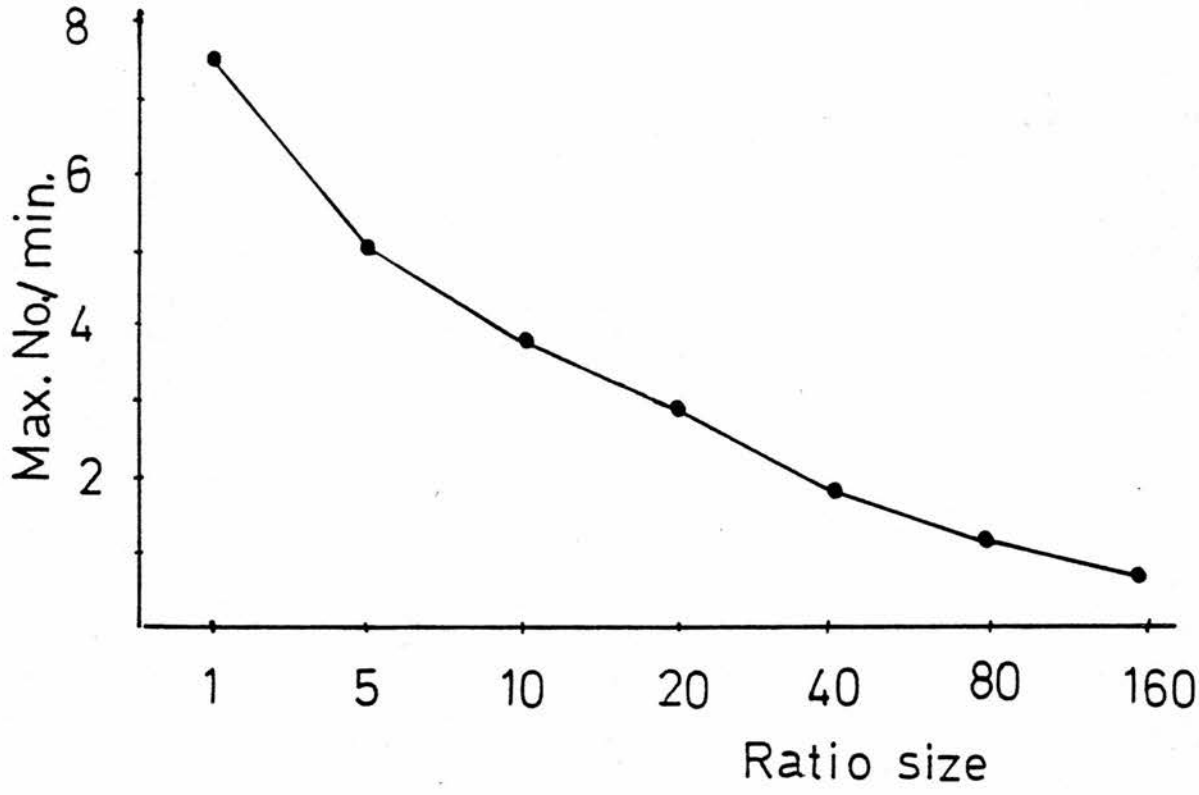

Mean Minimum IRI (secs)
100
80
60
40
20
10
20
40
80
160
Ratio Size

Figure 106

The maximum rate of reward earnings (per min.) at each ratio size. These points were derived from the actual mean minimum inter-reinforcement intervals (IRI) which occurred in ratios 10 - 160, shown in Figure 105. Maximum rewards per minute was computed for each ratio from 60/ minim. IRI. The minimum IRI's for ratios 1 and 5 were obtained by extrapolation.

Figure 107

The size of reinforcements over fixed ratios relative to their value at fixed ratio 1.


Max. No./ min.
8
6
4
2
1
5
10
20
40
80
160
Ratio size

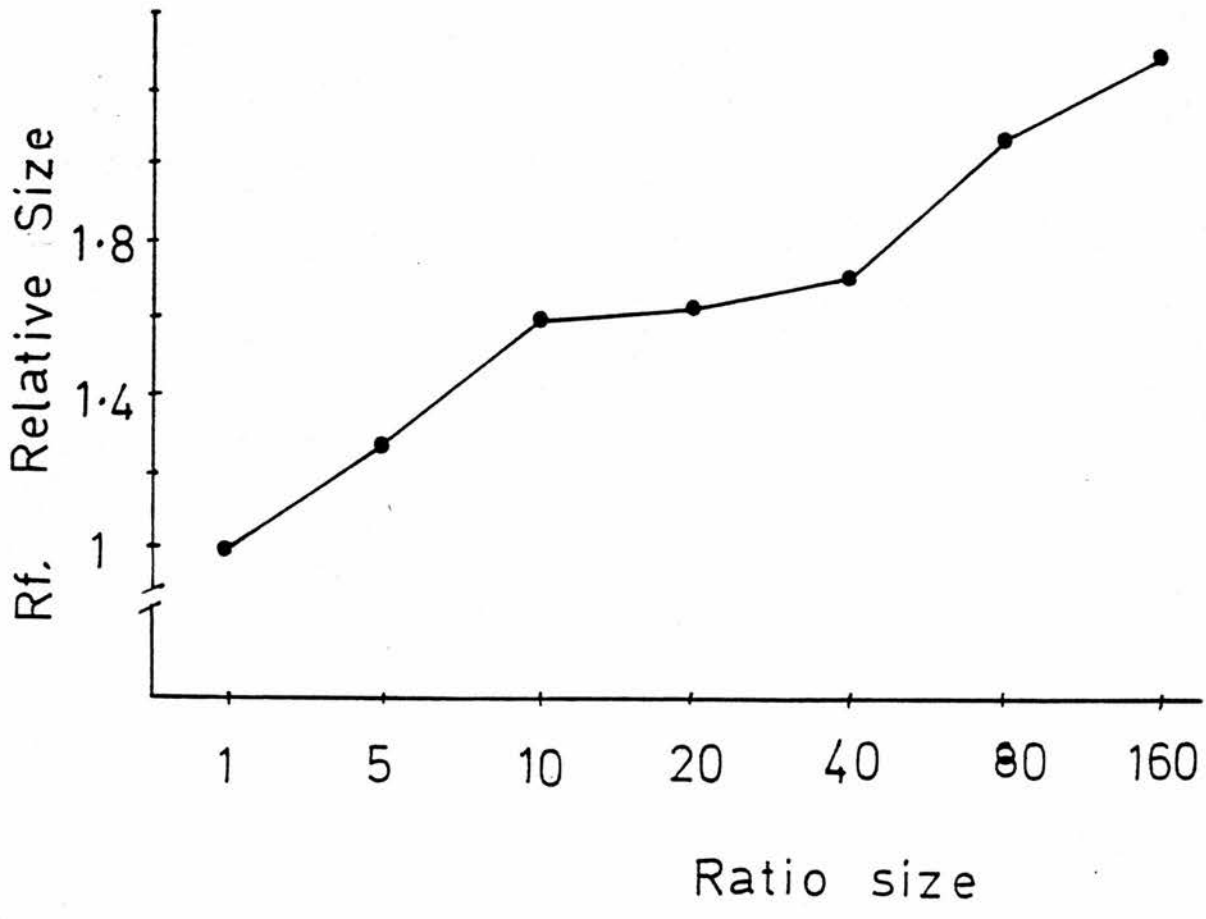

Rf. Relative Size
1·8
1·4
1
1
5
10
20
40
80
160
Ratio size

Figure 108

Changes in the maximum rate of food intake with increases in ratio size. An estimate of the maximum rate of intake at each ratio is obtained from the product of the maximum rate of reward earnings and the relative size of reward at that ratio. Note that because of the increase in reward value (relative size) the decrease in the maximum rate of intake is considerably slower for ratios 5 - 20 than it would be if determined by maximum reward rate alone.

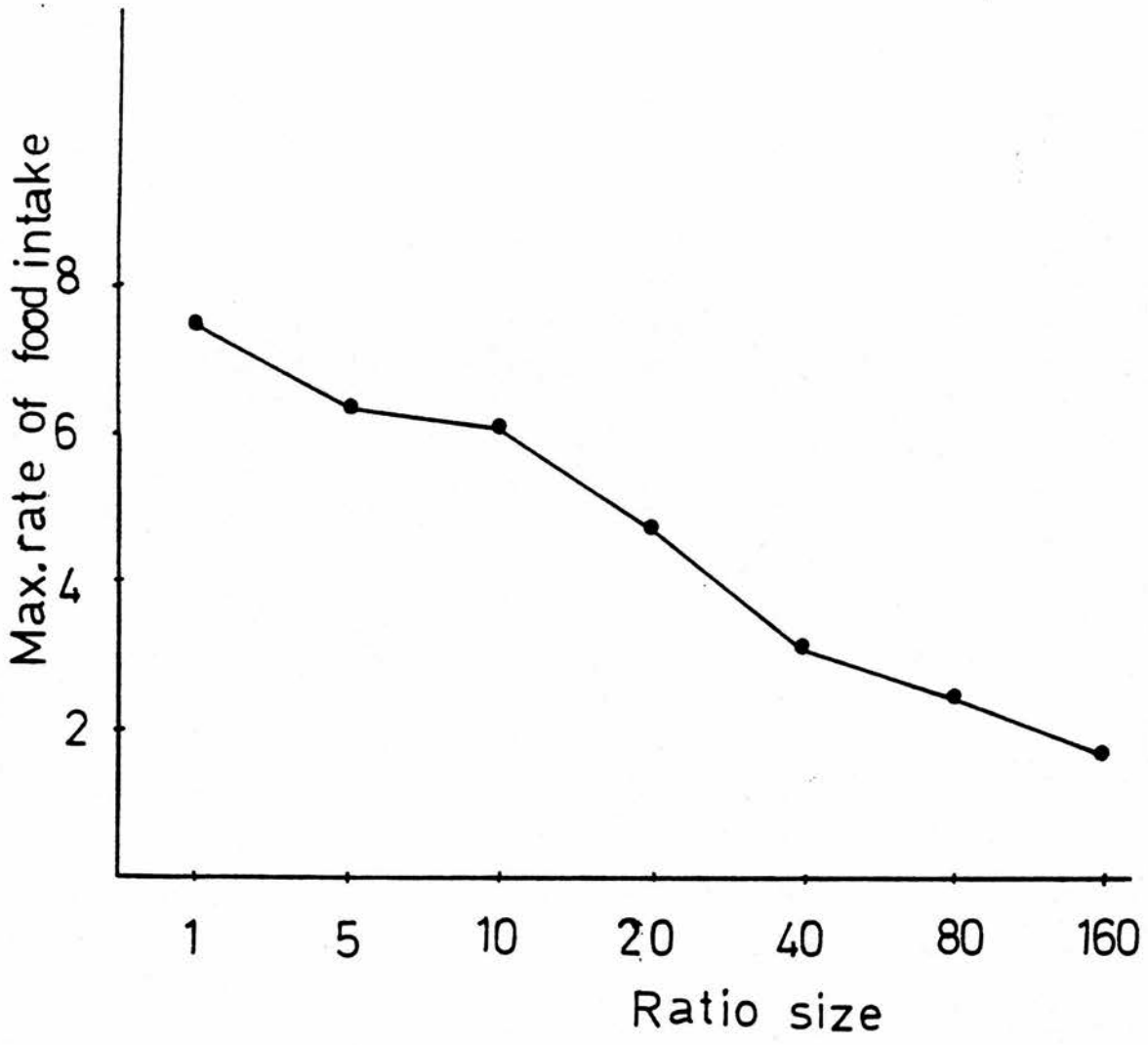

Max. rate of food intake
8
6
4
2
1
5
10
20
40
80
160
Ratio size

Table 38

The significant post-prandial and pre-prandial correlations occurring with changes in fixed ratio size. Correlation coefficients and significance levels are given in Appendix 7.

Significant pre-prandial correlations, p<

Bird	1	5	10	20	40	80	160	10	Ratio
Blank					.01				
F355G	.05				.001				
F67G									
F206G									
F6875					.001	.05		.05	

Significant post-prandial correlations, p<

Bird	1	5	10	20	40	80	160	10	Ratio
Blank		.001	.05	.001				.001	
F355G		.001	.001			.005		.05	
F67G		.05	.001					.05	
F206G	.01	.001	.001	.05	.001			.01	
F6875	.05	.001	.001						

CHAPTER 14

14.1 The Control of Operant Responding for Display Reward in Betta Splendens

The aim of the present thesis was to throw light on the nature of the system underlying aggressive reinforcement in Betta splendens, in the hope that detailed analysis of a single system would provide insight into the way in which explanation of reinforcer differences might be approached. The strategy adopted in attempting to determine the nature of the system underlying aggressive display in Betta splendens was to investigate the causation of the learned behaviour (the operant) by using methods similar to those used in the causal analysis of other behaviours (e.g. displays).

The starting point taken for investigation of the causation of Betta splendens operant behaviour was the observation by Bols (1977) and in this laboratory, that male conspecifics, particularly when not displaying, would elicit fear-like behaviour in displaying males. Bols (1977) interpreted these behaviours as caused by fear, on the basis of their morphology. Their occurrence in inter-male aggressive encounters, and during rewards in the instrumental situation led to the conclusion that aggression reward controlled operant behaviour by virtue of its action on two systems, aggression and fear. However, investigations of causation of fear-like behaviours in this thesis, revealed that they were morphologically similar to behaviour elicited by a reproductive female and causally related to reproductive condition. It was concluded that the motivational system underlying these behaviours was sexual in nature at a gross level of analysis, and inhibited by aggressive display in the conspecific. This view allowed control of these behaviours for the purpose of operant experiments, and removed the necessity for postulating a fear dimension in the control of operant behaviour by display reward.

Investigations of the control of operant behaviour for

display revealed that reward-elicited behaviours differed in their relations with the operant response. Some of these behaviours were inhibitory with respect to operant response-inhibiting post-reward behaviours, while another facilitated these. Only a single behaviour, a measure of general activity, was unrelated to post-reward behaviours. In addition, with the exception of this latter behaviour, all reward-elicited behaviours, in addition to controlling operant responding (the inter-reward interval) directly or indirectly (via post-reward behaviours), were themselves determined by the stimulus inter-presentation interval. The nature of the systems underlying most response-controlling displays and attack was found to be such that the conspecific caused excitory processes which first increased and then decayed after the termination of stimulation. The course of extinction and fixed ratio performance could both be explained by reference to these excitation and decay processes, since they involved imposed increases in the inter-reinforcement interval.

14.2 The Possible Function of Display Reward

Implicit in discussions of fixed ratio compensation is the idea that failure to compensate for display reward is in some sense a failure or inadequacy of the underlying system. Although the possible evolution and hence function of the ability to learn an instrumental behaviour for this reward has never been considered, it is implied that the system "should" compensate. It may be useful to consider how a system with the properties revealed by the investigations reported here, would operate in the wild. This speculation may serve to stimulate hypotheses and to demonstrate that the absence of FR compensation could be considered to be a "positive" adaptation to a particular kind of environment.

In the wild, a Betta splendens male may patrol its territory as it does in the laboratory. However, in the

wild Betta nests on the outer litoral zone, and is never observed swimming in open water during the nesting (territorial) phase (Forselius, 1957, p. 509). The range of visibility may be limited in such conditions. If the territory covers an area greater than the radius of visibility about the nest, intruding fish may be encountered in the territory where they could not be seen from the nest site. Indeed the very existence of patrolling suggests that this hypothesis is a plausible one. In addition to this, the outer areas of the territory may differ in the probability that they may conceal an intruder, a reasonable assumption if the territory is bordered by the territories of several individuals. In such circumstances, it may be adaptive to distribute patrolling activity such that most activity occurs at those areas most likely to be intruded upon. If patrolling is a costly activity, as it may be when nests from which the residident is absent are destroyed by conspecifics, then selective pressure would exist for this. Since the danger of intrusion in different areas of the territory presumably fluctuates, the basis for the evolution of a learning capacity may exist. That learned patrolling would come partly under the control of attack tendencies is easily accepted.

The effect of a schedule of intermittent reinforcement on such a system in the wild can now be considered. If reinforcement (a fight) serves to increase, by learning and by motivation, the patrolling time allocated to the site of that fight, then it might be expected that patrolling time allocated would fall when the proportion of rewards to visits falls. Contrary to this, the expectation of compensation for fixed ratio schedules implies the expectation that patrolling activity should increase.

14.3 Fixed Ratio Schedules and the Control of Feeding in the Barbary Dove

Investigation of fixed ratio performance for food reward

in the undeprived Barbary dove, revealed that with increasing fixed ratio the degree to which feeding was bouted first increased then decreased. This was accompanied by changes in the infrastructure of meals, such that intrameal facilitation in feeding failed to occur as FR was increased, and changes in the degree to which feeding was anticipatory occurred. This was explained by postulating a mechanism controlling food intake which involved positive feedbacks produced by contact with food. These decay between rewards, and since the increase in fixed ratio constrained the rate of food consumption, positive feedback decays increasingly between rewards as FR is increased. Thus, a breakdown in meal structure occurred.

The similarity between the effect of FR schedules on the intrameal structure of responding for food reward in the Barbary dove and the intra-session pattern of responding for display in Betta splendens, is striking. This similarity may be accounted for by the existence of excitation-decay processes in both systems. Since the factors responsible for the initiation of meals (meal frequency) and the persistence of feeding within meals (meal size) may differ (Wiepkema, 1971), the similarity between aggression and feeding systems may extend only to processes involved in persistence or the momentum (McFarland, 1971, p. 69) of the behaviour, and not to all processes (e.g. deprivation, steady-state error) operating after periods during which positive feedbacks have decayed considerably.

No evidence was found to support the hypothesis that FR compensation is produced by inter-meal deficit in this species. However, Barbary doves can learn to overeat to anticipate periods of low availability or high energetic demand (MacLeod, 1978, ch. 8 & 9), and the possibility that these processes may be involved in responding to the demands of the operant situation deserves further investigation.

14.4 The Comparison of Performance for Different Reinforcers

Hogan (1976) and Hogan et al. (1970) suggested that differences between aggression and food in their reinforcing properties may be attributable to differences in the motivational systems underlying these. Although having more to recommend it than an hypothesis based on the "biological necessity" of the commodities with which the systems are concerned (Shettleworth, 1972) the "motivational systems differ" view has contained an implicit assumption which may have caused theoretical problems. This same assumption is also encountered in the literature concerned solely with questions of reinforcement. Control theorists have treated motivational systems in terms of "design characteristics" which are seen as specifiable once the end-point or function of the system is known (Toates and Archer, 1978). This view may be simplistic. Taking the problem of food intake control, specifying the way in which an animal will solve the problem purely from the known functional end-point (e.g. body weight maintenance) usually leads to the inferring of a "set-point". This set point is usually seen in terms of a body weight or a level of circulating metabolites, deviation from which in some way determines the initiation and termination of eating. Such a system would indeed function adequately. However, some animals solve the problem more elegantly. Cats and Guinea pigs, for example, rely on bulk rather than caloric content, as an indicator of the amount they have eaten (Kanarek, 1975; Hirsch et al., 1978; Hirsch, 1973). These animals are similar in one respect, that is in their own ecological circumstances their food is relatively homogeneous with respect to caloric density. There is therefore, a high correlation between bulk ingested and calories ingested. An elaborate set-point system is unnecessary because of this ecologically afforded high correlation between calories and bulk. That these species do not increase their food intake in response to caloric dilution is not an inadequacy of the system,

but rather demonstrates its dependence for adequate functioning on a particular environmental relation. When this relation is experimentally altered, the "failure" of the system results.

Given that an adaptive mechanism may depend for its functioning on the environmental variables and relations on which it has evolved to depend, and given that even similar functional end-points may be achieved by systems differing in their use of environmental lawfulness, the operant situation appears in rather a new light. Different species and motivational systems are being placed in a supposedly "constant" environment - the Skinner box. However, the implications of this environment for the functioning of differentially supported systems may be quite different.

Problems for reinforcement theories may therefore arise from two sources. Firstly, there is a lack of knowledge about functional end-points. For example, it is not clear why aggressive displays occur (c.f. Caryl, 1979), neither is the Skinner box or runway likely to give much information about the role of display reward in Betta's territorial behaviour. The second source of difficulty for the explanation of reinforcement effects is the failure to consider organism-ecology relationships, instead attempting to discuss adaptive mechanisms in isolation. How to analyse organism-environment relations remains a problem for comparative psychology (but see e.g. McFarland, 1976).

In the area of reinforcer comparisons the possibility has only recently been considered that motivational systems may differ irrespective of their similarity of function (Hogan and Roper, 1978). Because of this, it was concluded that all explanation of performance differences for different reinforcers must necessarily be post-hoc. The view of organism-environment relations just considered and the results of the experiments reported in this thesis suggest that this may not be so.

If the role of a motivational system within its ecological and social context is known, then hypotheses can be generated about the lawfulness in that environment on which the system might depend for its control. Following this by experimental manipulation may then reveal the effective parameters of the environment which support various aspects of the systems functioning. Comparison of different systems then becomes meaningful, because such comparison is now with reference to a particular aspect of their functioning in relation to a particular environmental variable. The operant situation can then be analyzed with respect to this variable, and performance predictions can be made about differential effects of this variable on operant performance. Thus, the animal comes into the operant situations with certain motivational mechanisms which it evolved elsewhere. The question is, how do these interact with the characteristics of this new situation, and are different systems (species, or functional categories of behaviour) affected in the same way?

Since the function of feeding is relatively obvious, the experiment reported in this thesis which investigated the effects of fixed ratio size or food intake in the Barbary dove can be taken as an illustration of how this research could be conducted according to the above strategy. It could be hypothesised that feeding would involve positive feedback associated with contact with food, because of the existence of meals, and their structure outside the operant situation (after Wiepkema, 1971). The time course of the decay function associated with such feedback could be established outside the operant situation, by a method similar to that used for Betta's display and attack in ch. 10. Hypotheses could then be advanced about the response of such a system to a characteristic of all operant situations - the inter-reinforcement interval, and to reinforcement schedules which alter it. If another species

or reward type were shown to have a differing positive feedback function, then a difference in operant performance could be predicted accordingly.

14.5 Internal and External Control

Hogan and Roper (1978, p. 232) emphasize that the important point about Tinbergen's (1951, p. 124) model of the causation of behaviour, is that the central co-ordinating mechanism summates the internal and external influences to give the total motivation of the system. They conclude from this that the effects of internal and external factors are indistinguishable because one can substitute for the other. The dichotomy between internal and external factors is indeed one of doubtful theoretical validity (Baerends, 1971, p. 296) but this is only if "external" factors are viewed as stimuli, whose effects do not outlast their presentation.

Because some "external" sources of motivation may stimulate excitory processes which decay after stimulation according to a function which can be empirically determined, and "internal" factors might be expected to differ in the temporal course of their fluctuations, these are in fact distinguishable.

It has been suggested that comparisons of species or reinforcers in terms of operant performance, should follow non-operant motivational analysis. Such comparisons must not be in vacuo, but instead with reference to specific environmental variables and their implications for the functioning of particular aspects of the motivational systems in question. The lack of background information about the role of these systems in their natural setting is, however, a serious drawback since the framing of biologically appropriate questions must in consequence be based on intuitive considerations.

APPENDICES

Appendices 1 - 6 Behaviour over successive presentations at each inter-presentation interval (IPI).

Appendix

1 Biting (Bi) frequency
2 Butting frequency (Bu(f))
3 Butting duration (Bu(d))
4 Lateral display duration (LD(d))
5 Lateral display frequency (LD(f))
6 Air gulp frequency (AG(f))

Appendix 7

Table 1 : Pre-prandial correlations and fixed ratio schedule.
Table 2 : Post-prandial correlations and fixed ratio schedule.

Appendix 1 (Biting frequency)

Table 1

IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	70.5
2	0	0	70.5
3	.1	.1	79.5
4	.3	.2	94.0
5	.9	.3	157.0
6	.5	.2	109.5
7	.3	.2	93.0
8	.7	.4	124.5
9	1.1	.4	155.0
10	.6	.3	116.0
11	1	.4	142.5
12	1.1	.3	164.5
13	.8	.2	143.0
14	.7	.3	131.0
15	1	.4	143.5
16	1.7	.4	202.0
17	2	.4	226.5
18	1.3	.5	160.5
19	1.2	.4	165.5
20	.8	.3	146.0
21	1.3	.4	172.5
22	1.8	.5	195.0
23	1.5	.4	190.0
24	2.1	.6	224.5
25	2	.6	215.0
26	1.4	.5	185.0
27	1.7	.6	178.5
28	1.1	.5	164.5
29	2.5	.7	228.0
30	1.8	.5	202.5

Chi = 79.2383
df = 29
$p < .001$

Table 2

IPI(1)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	58.0
2	.2	.1	74.0
3	.5	.2	99.0
4	.7	.4	107.5
5	.6	.4	101.0
6	.9	.4	110.5
7	.6	.2	106.0
8	1.2	.4	147.0
9	1.4	.5	153.0
10	1.4	.4	156.0
11	1.4	.5	150.5
12	.8	.3	106.5
13	1.2	.5	144.5
14	1.3	.4	143.5
15	1.8	.7	164.0
16	1.3	.4	144.0
17	2	.5	187.5
18	2.1	.5	197.5
19	2.6	1	202.5
20	1.2	.4	147.5
21	2.4	.7	205.5
22	1.6	.5	153.0
23	2.3	.6	212.5
24	1.8	.8	159.5
25	2.9	.6	224.5
26	2	.4	203.5
27	2.2	.5	203.0
28	1.9	.6	177.0
29	2.1	.7	182.0
30	2.7	.5	229.0

Chi = 75.9368
df = 29
$p < .001$

Table 3

IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	75.5
2	.1	.1	80.5
3	.1	.1	83.5
4	.3	.2	104.0
5	0	0	75.5
6	.3	.2	108.5
7	.8	.3	143.5
8	.6	.2	126.5
9	1.2	.6	156.0
10	1.8	.5	213.0

Table 4

IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	95.5
2	.2	.1	117.5
3	.2	.2	114.5
4	.2	.1	117.5
5	.3	.2	126.5
6	.2	.2	114.5
7	.1	.1	108.5
8	.4	.2	139.0
9	.5	.3	137.0
10	.5	.2	148.5

Appendix 1 (Biting frequency)

Table 3

IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
11	1.3	.5	175.5
12	1.2	.4	165.0
13	1.1	.6	148.5
14	1.0	.5	141.0
15	1.1	.3	174.5
16	.5	.3	113.0
17	1.7	.8	168.0
18	1.1	.5	162.0
19	1.0	.4	155.5
20	1.3	.4	180.0
21	1.6	.6	184.0
22	1.0	.4	152.0
23	1.5	.4	188.5
24	.9	.3	152.5
25	1.1	.3	169.5
26	1.7	.5	199.5
27	1.8	.4	221.0
28	1.4	.4	192.0
29	1.9	.4	217.5
30	1.9	.4	224.0

Chi = 70.5586
df = 29
$p < .001$

Table 4

IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
11	.5	.2	147.5
12	.9	.3	174.5
13	.9	.3	176.0
14	.7	.3	163.0
15	.8	.3	166.0
16	1.3	.6	180.5
17	.7	.3	159.5
18	.9	.4	169.5
19	1.2	.5	196.5
20	.7	.4	156.0
21	.9	.3	178.5
22	.7	.3	155.0
23	.8	.3	158.0
24	1.0	.4	182.0
25	.7	.3	159.5
26	.7	.4	156.0
27	1.1	.5	185.5
28	1.3	.5	202.5
29	.7	.4	150.5
30	1.5	.5	214.5

Chi = 32.2
df = 29
$p < .30$

Table 5

IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	112.0
2	0	0	112.0
3	.1	.1	125.5
4	0	0	112.0
5	.4	.2	156.0
6	.1	.1	125.5
7	.6	.3	168.0
8	.4	.3	145.0
9	0	0	112.0
10	.3	.2	142.0
11	.8	.3	189.5
12	.6	.3	173.5
13	.4	.3	147.5
14	.2	.1	135.5
15	.5	.2	168.5

Table 5 continued.

Presentation	$\bar{X}$	SEM	Total Ranks
16	.4	.1	161.5
17	.3	.2	140.0
18	.4	.2	162.5
19	.5	.3	158.5
20	.8	.3	199.5
21	.2	.1	136.0
22	.2	.1	140.5
23	1.1	.4	197.5
24	.7	.4	178.0
25	.5	.2	168.0
26	.4	.2	158.0
27	1.0	.4	207.0
28	.4	.2	159.0
29	.7	.4	171.0
30	.7	.3	188.5

Chi = 27.3877
df = 29
$p > .50$

Appendix 2 (2 pages) Butting frequency.

Table 1
IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.1	.1	60.0
2	.5	.3	74.5
3	.8	.5	86.5
4	.8	.3	97.0
5	1.1	.2	119.0
6	1.6	.4	146.0
7	.9	.2	107.0
8	1	.4	98.0
9	1	.3	108.5
10	1.8	.7	139.0
11	1.7	.5	146.0
12	2.2	.6	171.0
13	1.8	.6	143.5
14	2.4	.7	180.5
15	3	.7	218.5
16	2.3	.6	179.5
17	2.6	.4	208.5
18	2	.4	169.0
19	2.5	.7	194.5
20	1.4	.3	135.0
21	1.9	.6	161.0
22	2.8	.6	212.5
23	2.6	.7	195.0
24	2.9	.8	202.5
25	2.1	.6	169.0
26	1.9	.6	157.5
27	3	.9	201.5
28	2.5	.8	190.0
29	2.9	.8	201.0
30	2.6	.8	178.5

Chi = 73.7244
df = 29
$p < .001$

Table 2
IPI(1)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.3	.2	78.0
2	.3	.2	59.5
3	.4	.2	81.0
4	.4	.2	67.0
5	.7	.3	84.0
6	1.3	.5	106.0
7	1.4	.5	114.0
8	1.5	.5	122.0
9	1.9	.8	136.5
10	1.7	.5	147.5
11	2.3	.8	161.5
12	1.8	.6	147.5
13	1.8	.6	127.0
14	2.4	.4	155.5
15	2.7	.8	181.0
16	2.2	.6	178.5
17	2.6	.4	165.0
18	3.0	.7	200.5
19	2.6	.7	204.5
20	2.0	.7	193.5
21	3.0	.8	144.0
22	2.6	.7	204.5
23	2.4	.7	181.0
24	3.2	1.3	178.0
25	2.8	.6	193.0
26	2.6	.6	189.0
27	3.3	.8	194.0
28	2.7	.8	229.5
29	3.0	.7	193.5
30	3.2	.9	206.5

Chi = 84.4277
df = 29
$p < .001$

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	69.5
2	0	0	69.5
3	.4	.2	105.5
4	.9	.4	133.5
5	0	0	69.5
6	.7	.2	118.0
7	1.2	.5	127.5
8	1	.4	129.5
9	1.6	.6	160.0
10	1.9	.7	176.0
11	1.0	.4	131.5
12	1.3	.5	144.0

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	84.0
2	.3	.2	103.0
3	.3	.3	102.5
4	.7	.4	129.0
5	1.4	.8	153.0
6	1	.6	131.5
7	.8	.4	119.0
8	.9	.6	127.0
9	1.3	.8	144.5
10	1.1	.8	131.5
11	1.3	.8	144.5
12	1.2	.8	133.0

Appendix 2 (continued)

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
13	1.8	.8	162.0
14	1.8	.8	161.5
15	2.1	.4	204.0
16	1.1	.5	132.5
17	1.8	.6	170.5
18	2.5	.8	212.5
19	1.6	.7	150.0
20	2.4	.8	204.0
21	1.7	.7	164.0
22	2.4	.8	195.5
23	2	.8	166.5
24	1.7	.8	150.0
25	1.5	.5	158.0
26	2.5	.8	217.0
27	1.8	.2	160.5
28	2.2	.6	184.5
29	2.4	.6	207.5
30	2.7	.8	214.5

Chi = 65.3677
df = 29
$p < .001$

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
13	1.5	.9	154.0
14	2	.8	198.5
15	1.7	.7	180.0
16	2	.8	192.0
17	1.9	.9	189.0
18	1.2	.6	151.5
19	1.7	.6	174.0
20	1.5	.9	146.5
21	1.8	.8	168.0
22	1.7	.7	180.0
23	1.6	.7	180.0
24	1.7	.8	181.5
25	1.4	.7	149.0
26	1.6	.6	181.5
27	1.5	.7	149.0
28	2.7	1.2	209.5
29	2	.7	189.0
30	2	.5	201.5

Chi = 37.5720
df = 29
$p > .10$

Table 5
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.1	.1	115.5
2	0	0	101.0
3	.3	.2	129.5
4	.3	.2	126.0
5	.4	.2	148.5
6	.4	.3	129.5
7	.3	.2	124.5
8	.4	.2	139.0
9	.2	.2	116.0
10	.1	.1	114.5
11	.5	.2	151.5
12	.9	.4	184.5
13	.4	.2	138.5
14	.3	.3	122.0
15	.9	.3	189.0

Table 5 (contd.)
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
16	.7	.3	168.0
17	.7	.3	166.5
18	.9	.3	192.5
19	.7	.4	158.0
20	1.0	.4	182.5
21	.4	.3	135.5
22	.4	.3	134.5
23	1.7	.6	214.5
24	1.2	.5	192.5
25	.3	.2	130.0
26	.8	.3	176.5
27	1	.4	179.5
28	.9	.2	191.5
29	1.5	.6	197.0
30	1.2	.5	201.5

Chi = 38.1587
df = 29
$p > .10$

Appendix 3 (Butting duration (secs.))

Table 1
IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.02	.02	55.5
2	.8	.6	79.5
3	.8	.6	85.5
4	1.4	.7	108.5
5	1.1	.5	118
6	1.8	.6	142.5
7	.8	.3	111.0
8	.8	.4	87.0
9	.9	.3	101.8
10	2.9	1.4	139.5
11	2.8	1.1	140.5
12	2.8	1.1	140
13	4.2	1.7	155
14	3.7	1.4	146
15	5.5	2	188.5
16	5.5	2.3	179.5
17	6.6	2.5	210.5
18	6.6	2.6	216.0
19	6.5	2.1	218.5
20	5	3	162.0
21	5.7	3.1	182.5
22	5.4	2.4	157.5
23	7.7	3.2	200
24	6.8	2.9	192
25	4.4	1.8	162
26	7.5	2.7	201
27	6.6	2.8	205.5
28	7.3	3	201
29	5.1	1.9	180.5
30	5.8	2.1	183.5

Chi = 76.6528
df = 29
$p < .001$

Table 2
IPI(1)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.2	.1	78.0
2	.2	.2	60.5
3	.6	.4	92.5
4	.7	.4	71.5
5	.9	.4	87.0
6	2	1.3	102.5
7	1.4	.6	101.5
8	1.6	.5	123.5
9	2.2	1.0	118.0
10	2.7	1.4	139.0
11	3.1	1.3	134.5
12	2.3	.9	136.5
13	2.5	1.2	112.5
14	3.4	1.0	187.5
15	5.1	2.7	178.5
16	3.9	1.7	171.0
17	4.3	1.0	197.0
18	6.3	2.3	221.5
19	5.1	2.2	202.5
20	5.1	1.9	172.0
21	7.5	2.9	230.5
22	5.3	2.3	187.0
23	5.2	2.1	186.5
24	7.5	3.3	206.5
25	4.4	1.5	177.0
26	3.9	1.2	172.0
27	7.1	2.4	238.0
28	3.6	1.4	157.0
29	5.5	1.6	202.0
30	5.5	1.7	206.0

Chi = 96.2671
df = 29
$p < .001$

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	70.0
2	0	0	70.0
3	.2	.1	105.0
4	.9	.5	129.0
5	0	0	70.0
6	.6	.2	123.0
7	1.5	.7	113.5
8	.8	.3	129.5
9	2.7	1.1	154.5
10	3.2	1.5	144.0
11	2.4	1.5	144.0
12	2.3	1.4	135.5
13	4.8	2.4	175.5

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	0	0	84.5
2	.2	.1	103.0
3	.2	.2	105.0
4	.5	.3	119.5
5	1.3	.9	131.0
6	.6	.3	141.0
7	.8	.6	117.5
8	1.1	.8	129.0
9	1.4	1.1	129.5
10	1.8	1.6	141.0
11	1.9	1.5	136.0
12	1.7	1.6	125.5
13	2.2	1.6	142.0

Appendix 3 (continued)

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
14	4	1.9	163.5
15	4.2	1.5	209.0
16	2.5	1.4	141.5
17	3.5	1.5	162.5
18	5.7	2	202.5
19	2.7	1.5	132.5
20	4.5	1.9	185.5
21	3.6	2	161.5
22	5.8	2.4	209.5
23	5.6	2.9	169.0
24	3.7	1.8	136.5
25	4.3	1.9	182.5
26	5	2	222.0
27	5	2.5	173.0
28	5.7	2.3	204.0
29	5.6	2.7	215.0
30	4.4	1.9	203.5

Chi = 69.1929
df = 29
$p < .001$

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
14	3	1.6	189.0
15	2	1.0	157.0
16	2.3	1.5	182.0
17	2.9	1.7	185.5
18	2.5	2.2	165.0
19	2.4	1.5	166.0
20	3.5	1.9	160.0
21	3.0	1.8	162.5
22	3.5	1.7	212.0
23	4.2	2.5	176.0
24	2.3	1.9	173.0
25	2.5	1.8	152.0
26	2.6	1.2	187.0
27	2.2	1.2	154.0
28	3.6	1.6	187.0
29	4.7	2.2	218.0
30	4.5	2.2	219.5

Chi = 43.6875
df = 29
$p < .05$

Table 5
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	.1	.1	115.5
2	0	0	101.0
3	.2	.2	132.0
4	.2	.1	128.0
5	.2	.1	146.5
6	.9	.7	140.5
7	.5	.5	126.5
8	.2	.1	138.0
9	.1	.1	114.0
10	.1	.1	116.0
11	.2	.1	152.0
12	.6	.2	179.5
13	.3	.2	144.0
14	.3	.4	125.5
15	.5	.2	185.5

Table 5 continued
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
16	.7	.4	168.5
17	1.1	.6	174.0
18	.8	.4	195.0
19	.9	.6	162.5
20	.8	.5	175.5
21	.4	.3	139.0
22	.5	.4	141.5
23	1.3	.5	199.5
24	.9	.4	179.5
25	.2	.1	127.0
26	.6	.3	175.0
27	.7	.3	171.0
28	.9	.4	193.0
29	1.3	.5	194.5
30	1.5	.7	210.5

Chi = 33.5269
df = 29
$p > .20$

Appendix 4 (2 pages) for Figs. 63 - 67, Lateral display duration.

Table 1
IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	9.0	1.9	199
2	9.9	1.8	215
3	10.8	2.4	208
4	9.1	2	195
5	10.3	2.5	195
6	10.2	1.8	208
7	9.4	3.1	191.5
8	8.3	2.2	196
9	7.9	2.3	177
10	5.8	2.1	147.5
11	5.9	1.9	148.5
12	6.8	1.3	171.5
13	7.1	2.4	153
14	6.2	1.9	127.5
15	7	2.6	134.5
16	7.5	3.4	143.5
17	5.8	1.9	122.5
18	5.8	2.5	128
19	7.3	2.7	161.5
20	6.9	2.3	139
21	5.4	1.8	121.5
22	8.2	2.2	196.5
23	4.9	1.7	114
24	7.1	2	164
25	4.8	2	109.5
26	3.8	2.3	56.5
27	5.8	1.9	151
28	4.6	1.1	107
29	5.9	2.3	117
30	7.2	2.9	151.5

Chi = 53.9010
df = 29
$p < .01$

Table 2
IPI(1)

Presentation	$\bar{X}$	SEM	Total Ranks
1	14.3	2.9	237.0
2	7.1	1.4	214.0
3	7.2	1.5	175.5
4	10.8	1.8	209.5
5	7.4	2.5	171.0
6	7.1	1.8	166.5
7	8.0	2.1	172.0
8	6.4	1.9	174.0
9	7.3	2.6	159.5
10	8	1.9	192.0
11	6.9	1.9	174.0
12	8.0	2.3	183.5
13	6.9	1.9	153.5
14	7.5	2.1	169.0
15	5.5	1.8	107.0
16	5.6	2.1	109.5
17	6.1	0.7	142.0
18	7.1	1.7	179.5
19	6.8	1.6	170.0
20	4.8	1.8	97.5
21	6.1	2.1	136.0
22	6.8	2.2	155.5
23	5.6	1.6	102.5
24	5.6	2	117.0
25	7.1	1.7	108.0
26	4.6	1.6	136.5
27	6.8	2.5	121.5
28	4.8	1.7	124.0
29	5.2	1.6	121.5
30	5.8	1.9	

Chi = 47.2817
df = 29
$p < .02$

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	12.8	2.1	213.5
2	10.5	1.5	205.5
3	12.5	2.5	240.5
4	10.3	1.3	208.0
5	11.2	2.2	227.0
6	9.3	1.8	197.0
7	8.4	1.8	163.5
8	8.2	1.9	155.0
9	9.4	2.1	184.0
10	9.2	2.1	185.0

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	11.1	1.1	221.5
2	8.8	1.6	168.0
3	10.3	1.1	206.0
4	12.1	1.6	242.0
5	9.0	.9	183.0
6	9	1.6	186.5
7	9.7	1.9	191.0
8	8.9	1.8	194.5
9	10.4	1.6	217.5
10	9.4	1.6	190.5

Appendix 4 contd.

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
11	6.4	2.2	135.0
12	7.1	2.1	147.5
13	8.2	1.9	175.0
14	8.8	2.2	182.5
15	7.8	2.3	144.5
16	7.8	2.5	142.0
17	7.4	1.3	165.5
18	5.8	1.7	111.5
19	6.5	2.2	121.0
20	5.5	1.3	123.5
21	8.7	2.3	163.5
22	5.2	1.3	103.5
23	6.3	1.7	137.0
24	6.1	1.8	115.0
25	6.6	1.4	144.5
26	5.8	1.7	111.0
27	5.2	1.0	128.0
28	4.9	1.3	103.5
29	5.9	2.4	100.5
30	5.2	1.5	116.0

Chi = 58.6257
df = 29
$p < .001$

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
11	10.5	2.0	215.5
12	6.7	1.7	129.0
13	6.3	1.5	106.5
14	7.0	1.6	129.0
15	7.5	1.4	145.0
16	7.8	1.5	144.5
17	7.6	1.7	154.5
18	7.7	1.6	149.0
19	9.5	1.6	189.0
20	8.2	2.3	147.0
21	6.4	1.6	114.0
22	5.7	1.5	87.5
23	6.1	1.2	109.0
24	7.4	2.1	150.0
25	6.8	1.7	110.0
26	6.4	1.1	130.5
27	6.4	1.7	106.0
28	4.8	1.7	57.0
29	7.6	1.9	134.0
30	7.3	2.1	142.5

Chi = 73.5444
df = 29
$p < .001$

Table 5
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	16.1	2	229.0
2	13.6	1.8	189.0
3	14.4	1.9	224.5
4	12.4	1.8	199.5
5	12.6	2.4	180.5
6	11.9	1.7	185.0
7	9.4	1.6	131.5
8	10.9	1.4	183.0
9	9.9	1.6	143.0
10	12.4	1.8	198.0
11	11	1.6	164.5
12	12.4	1.6	205.0
13	11	1.6	164.5
14	10	1.5	137.5
15	11.1	1.4	180.5

Table 5 contd.
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
16	12	1.5	192.5
17	9.7	1.6	122.0
18	10.4	2.1	154.5
19	9.3	1.6	112.5
20	10.9	2.0	157.5
21	8.	1.4	113.0
22	10	1.6	142.0
23	8.2	1.1	106.0
24	10.5	1.2	158.0
25	8.1	1.8	96.5
26	8.9	1.7	116.0
27	10.9	1.8	96.5
28	7.7	1.4	110.5
29	7.7	1.7	102.0
30	7.6	1.5	98.5

Chi = 56.2436
df = 29
$p < .01$

Appendix 5 (2 pages) for Figs. 69 - 73, Lateral display frequency (LD(8)).

Table 1
IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	4.1	.6	176.0
2	4.0	.3	181.0
3	3.6	.7	149.5
4	3.7	.6	166.5
5	3.6	.8	163.0
6	4.7	.9	203.0
7	3.1	.7	122.5
8	3.8	.7	165.5
9	4.0	.7	183.5
10	3.1	.4	135.5
11	3.5	.5	156.0
12	4.1	.8	191.5
13	3.6	.7	159.0
14	3.7	.7	165.0
15	3.5	.6	154.0
16	4.0	.7	185.0
17	3	.4	124.0
18	3.2	.6	139.5
19	3.4	.5	155.5
20	3.2	.4	141.5
21	2.7	.5	101.5
22	4.2	.4	210.0
23	3.4	.5	153.5
24	3.9	.7	172.5
25	3.1	.5	135.5
26	2.6	.6	98.5
27	3.2	.5	139.0
28	3.3	.7	139.0
29	3.2	.6	142.0
30	3.2	.5	137.0

Chi = 26.3096
df = 29
$p > .50$

Table 2
IPI(1)

Presentation	$\bar{X}$	SEM	Total Ranks
1	4.0	.6	156.0
2	3.9	.7	144.0
3	4.0	.9	135.5
4	5.2	1.0	182.5
5	4.1	.9	151.0
6	4.9	1.0	179.0
7	4.4	.6	178.0
8	4.4	.8	176.5
9	4.1	.6	161.0
10	4.1	.6	165.0
11	3.9	.6	155.0
12	4.1	.6	163.0
13	1.7	.9	185.0
14	4.5	.4	186.5
15	3.6	.7	126.0
16	3.5	.6	119.0
17	3.9	.8	149.0
18	4.4	.8	180.0
19	5	1.0	194.5
20	2.9	.5	94.0
21	4.3	1.1	155.0
22	3.8	.5	149.0
23	3.4	.6	125.5
24	4.3	1.3	121.0
25	4.4	.8	184.0
26	2.9	.5	106.5
27	4	.7	148.5
28	4.4	1.1	143.0
29	4.7	.9	163.5
30	4.2	.9	173.0

Chi = 24.3257
df = 29
$p > .70$

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	4.2	.6	177.0
2	4.1	.5	177.0
3	4.9	.6	216.0
4	5.3	.7	233.5
5	4.1	.4	176.5
6	4.9	.6	219.5
7	3.7	.5	138.0
8	3.9	.7	155.0
9	4.1	.7	174.5
10	4.3	.8	185.5
11	3.1	.7	131.5
12	3.2	.6	133.0

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	3.7	.5	111.0
2	4.6	.8	151.0
3	5.3	.9	187.5
4	5.7	.7	200.0
5	5.1	.4	203.5
6	4.8	.7	174.5
7	3.8	.6	123.5
8	5.5	.5	221.5
9	5	.8	195.5
10	5.3	.8	202.5
11	5	.9	196.0
12	3.5	.5	106.0

Appendix 5 contd.

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
13	3.7	.5	162.0
14	3.6	.4	162.5
15	2.6	.5	106.0
16	3.1	.7	127.0
17	3.9	.5	168.0
18	3.1	.7	119.0
19	3.4	.5	132.0
20	3.3	.7	143.0
21	4	.8	165.0
22	2.9	.5	104.0
23	3.3	.7	138.5
24	3.9	.5	171.0
25	3.8	.7	166.0
26	3.9	.6	176.0
27	3.4	.6	155.0
28	2.7	.6	102.5
29	2.9	.7	111.5
30	2.9	.8	123.5

Chi = 42.5703
df = 29
$p < .05$

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
13	4.2	.5	152.0
14	3.5	.7	109.5
15	4.6	.4	171.5
16	4.4	.8	156.0
17	4.5	.6	167.0
18	4.2	.7	152.0
19	5.1	.6	167.0
20	4.7	.9	157.0
21	4	.7	134.0
22	4	.5	142.5
23	3.7	.6	114.0
24	3.9	.7	126.0
25	4	.7	140.0
26	4	.6	136.0
27	4.2	.4	141.0
28	3.4	.6	104.0
29	4.3	.8	140.5
30	4.1	.8	130.5

Chi = 43.0735
df = 29
$p < .05$

Table 5
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	5.0	.9	115.0
2	5.4	1	149.0
3	5.5	.7	151.5
4	5.5	1.0	167.5
5	5.2	.9	149.5
6	6.1	.8	176.5
7	5.8	1.1	167.0
8	5.8	1.0	172.5
9	6.2	1.3	165.5
10	6.4	1.0	194.0
11	5.1	.8	125.5
12	6.3	.8	193.5
13	6.3	.8	202.0
14	6	.6	174.5
15	6	.8	178.5

Chi = 26.2507
df = 29
$p > .50$

Table 5 contd.
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
16	5.5	.8	152.0
17	5.4	.7	139.5
18	6.2	.9	196.5
19	5.6	.6	155.5
20	6	1.0	176.0
21	5.6	.7	158.0
22	5.5	.8	144.0
23	4.5	.5	114.5
24	5.6	.8	144.0
25	4.9	.7	130.5
26	5.2	.7	141.5
27	5.7	1.0	172.0
28	4.7	.6	122.0
29	4.6	.8	121.5
30	4.3	.8	101.5

Appendix 6 (2 pages) Air gulp frequency (AG(f))

Table 1
IPI(0)

Presentation	$\bar{X}$	SEM	Total Ranks
1	1.5	.2	95.5
2	2.2	.5	166.5
3	2.0	.4	159.5
4	1.9	.4	134
5	1.7	.4	118
6	2.3	.5	163
7	2.2	.5	170.5
8	2.1	.4	158.5
9	2.5	.6	170.5
10	2.3	.3	165
11	2.2	.5	153.5
12	2.3	.5	170.5
13	1.8	.3	116.5
14	2.2	.5	162
15	2.4	.6	163
16	2.7	.5	204.5
17	2.1	.5	163.5
18	2.0	.5	146
19	2.4	.4	165.5
20	2.4	.4	173.5
21	2.4	.5	176.5
22	2.4	.5	173,5
23	2.1	.4	143
24	2.3	.5	158
25	2.1	.5	146
26	2.2	.5	151.5
27	2.3	.4	172.5
28	1.7	.5	106.5
29	2.2	.3	156
30	2.1	.4	147

Chi = 19.1321
df = 29
$p > .90$
Spear. with serial position
= .1871, $p > .05$

Table 2
IPI(1)

Presentations	$\bar{X}$	SEM	Total Ranks
1	1.6	.5	104
2	2.3	.6	130
3	2.2	.6	136
4	2.6	.5	154.5
5	2.3	.6	136
6	3.0	.7	189
7	2.9	.8	173.5
8	2.2	.5	127.5
9	2.4	.7	137
10	2.6	.4	163
11	2.0	.4	115.5
12	2.0	.6	109
13	3.0	.7	184
14	2.9	.6	183
15	2.8	.5	177.5
16	2.4	.5	144.5
17	2.4	.6	148
18	2.5	.7	156
19	3.7	.9	208.0
20	2.4	.4	143.5
21	2.7	.9	149.5
22	2.0	.4	121
23	2.3	.4	143.5
24	3.6	1.1	193
25	2.9	.5	179.5
26	2.0	.4	178
27	2.7	.5	168
28	2.5	.5	157
29	2.6	.4	169.5
30	2.7	.4	171

Chi = 25.9148
df = 29
$p > .50$
Spear. with serial position
= .3298, $p < .05$

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
1	1.3	.4	112.5
2	1.6	.4	145
3	1.7	.4	145.5
4	2.1	.7	161
5	1.5	.5	132
6	2.0	.5	169
7	1.8	.5	159
8	1.1	.3	90.5
9	1.4	.4	113
10	2.0	.4	176

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
1	1.5	.6	107
2	1.8	.5	129
3	2.6	.4	199.5
4	2.5	.5	180
5	2.2	.4	167
6	1.9	.5	125
7	1.7	.4	132.5
8	2.6	.5	194.5
9	2.0	.4	138.5
10	2.1	.4	154

Table 3
IPI(10)

Presentation	$\bar{X}$	SEM	Total Ranks
11	1.9	.3	171
12	1.3	.3	115.5
13	1.5	.5	128
14	1.7	.4	146.5
15	1.7	.3	149.5
16	1.3	.3	119.5
17	2.1	.4	181
18	1.5	.4	136
19	1.6	.4	135
20	1.8	.3	157
21	2.0	.4	176
22	1.6	.4	140.5
23	2.1	.5	177
24	2.2	.5	185.5
25	2.3	.5	193.5
26	2.5	.5	213.5
27	2.7	.6	224.5
28	1.7	.6	145.5
29	2.3	.4	198
30	1.9	.7	154

Chi = 36.4360
df = 29
$p < .01$
Spear. with serial position = .5066
$p > .10$

Table 4
IPI(30)

Presentation	$\bar{X}$	SEM	Total Ranks
11	2.4	.4	178.5
12	1.8	.3	119.5
13	2.6	.3	199
14	1.8	.3	122.5
15	2.1	.4	154
16	1.8	.4	125
17	2.0	.5	142
18	2.3	.4	164.5
19	2.3	.6	162.5
20	2.5	.6	162.5
21	2.5	.5	181.5
22	2.1	.4	167
23	2.2	.5	146.5
24	2	.6	144
25	2.5	.5	190
26	2.3	.6	151.5
27	2.3	.5	170.5
28	1.7	.5	117
29	2.3	.6	151
30	2.4	.6	174

Chi = 25.0122
df = 29
$p > .05$
Spear. with serial position = .1733 $p > .05$

Table 5
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
1	1.2	.3	91
2	1.8	.4	139
3	1.8	.3	141
4	1.4	.5	101
5	1.5	.4	121.5
6	1.8	.4	135.5
7	2.3	.3	181.5
8	1.6	.4	106
9	2.5	.4	197.5
10	2.5	.6	169.5
11	2.1	.5	154
12	2.1	.6	154.5
13	2.5	.6	180.5
14	2.4	.6	170
15	2.6	1.5	191

Table 5 contd.
IPI(70)

Presentation	$\bar{X}$	SEM	Total Ranks
16	1.7	.3	126
17	2.0	.5	144
18	2.3	.5	178.5
19	2.5	.5	181.5
20	2.1	.4	149.5
21	2.9	.5	211
22	1.5	.3	110
23	2.4	.6	176
24	2.4	.8	158.5
25	2.1	.7	141
26	2.9	.5	216.5
27	1.9	.5	130.5
28	2.2	.3	175
29	2.1	.5	149
30	2.3	.6	169.5

Chi = 37.8638
df = 29
$p > .10$
Spear. with serial position = .4047
$p < .05$

Appendix 7 (Table 1)

Pre-prandial correlation and ratio. Figures in brackets indicate significance levels.

Ratio	(1)	(5)	(10)	(20)
Bird				
Blank	-0.0892	0.4792	0.1248	0.0747
	(0.4417)	(0.4567)	(0.4516)	(0.4454)
F355G	0.1949	0.0655	0.1837	-0.0100
	(0.0447)	(0.6231)	(0.2522)	(0.9463)
F67G	0.1646	0.0146	-0.0760	-0.0086
	(0.1232)	(0.9191)	(0.5582)	(0.9477)
F206G	0.0541	-0.0553	-.0286	0.1039
	(0.5244)	(0.6031)	(0.7896)	(0.2578)
F687S	0.0431	-0.0832	-0.1513	0.0641
	(0.6447)	(0.3108)	(0.1435)	(0.4764)

Ratio	(40)	(80)	(160)	(10)
Bird				
Blank	0.2599	0.1412	0.1316	0.1771
	(0.0057)	(0.0958)	(0.1046)	(0.1184)
F355G	0.4186	-0.0508	0.0993	0.1762
	(0.0009)	(0.6179)	(0.2817)	(0.1179)
F67G	0.1224	-0.0692	0.0092	0.0236
	(0.2629)	(0.5480)	(0.9365)	(0.8470)
F206G	0.1156	-0.0789	0.0564	0.0920
	(0.1200)	(0.2457)	(0.4848)	(0.1752)
F687S	0.4039	0.2026	0.1332	0.1999
	(0.0000)	(0.0163)	(0.1039)	(0.0174)

Appendix 7 (Table 2)

Post-prandial correlation and ratio. Figures in brackets indicate significance levels.

Ratio	(1)	(5)	(10)	(20)
Bird				
Blank	0.7024	0.5805	0.3465	0.3478
	(0.0000)	(0.0004)	(0.0299)	(0.0004)
F355G	0.3230	0.5819	0.6205	-0.1800
	(0.0010)	(0.0000)	(0.0000)	(0.2153)
F67G	0.2041	0.3518	0.4999	-0.1788
	(0.0545)	(0.0104)	(0.001)	(0.1419)
F206G	0.2720	0.6092	0.5435	0.2330
	(0.0014)	(0.0000)	(0.0000)	(0.0130)
F687S	0.2061	0.2844	0.3860	0.1410
	(0.0255)	(0.0006)	(0.0002)	(0.1152)

Ratio	(40)	(80)	(160)	(10)
Bird				
Blank	0.0752	-0.1137	-0.0653	0.4764
	(0.4295)	(0.1815)	(0.4233)	(0.0000)
F355G	-0.0248	0.3151	0.1035	0.2631
	(0.8492)	(0.0018)	(0.2617)	(0.0182)
F67G	0.0180	-0.1989	-0.0573	0.3258
	(0.9801)	(0.0804)	(0.3994)	(0.0132)
F206G	0.3708	-0.0573	-0.0200	0.1778
	(0.0000)	(0.3994)	(0.8047)	(0.0086)
F6873	0.1178	0.1421	-0.0917	0.1357
	(0.1471)	(0.0936)	(0.2653)	(0.1084)

BIBLIOGRAPHY

ALLISON, J. (1976). Contrast, induction, facilitation, suppression and conservation. J. Exp. Anal. Behav. 25, 185 - 198.

ALLISON, J. and CASTELLAN, N.J.Jr. (1970). Temporal characteristics of nutritive drinking in rats and humans. J.Comp. Physiol. Psychol. 70, 116 - 125.

ANDREW, R.J. (1972). The information potentially available in mammal displays. In R.A. Hinde (Ed.), Non-verbal Communication. Cambr. Univ. Pr..

ASSEM, J. VAN DEN, and MOLEN, J. VAN DER (1969). Waning of the aggressive response in the 3-spined stickleback upon constant exposure to a conspecific. I. A Preliminary Analysis of the phenomenon. Behav. 34, 286 - 324.

BAENNINGER, R. (1966). Waning of aggressive motivation in Betta splendens. Psychon. Sc. 4, 241 -242.

BAENNINGER, L., BERGMAN, M. and BAENNINGER,R. (1969). Aggressive motivation in Betta splendens: replication and extinction. Psychon. Sc. 16, 260.

BAENNINGER, R. and MATTLEMAN, R.A. (1973). Visual reinforcement: operant acquisition in presence of a free mirror. Anim. Learning Behav. 1, 302 - 306.

BAERENDS, G.P. (1957). The ethological analysis of fish behaviour. In M.E. Brown (ed.) The Physiology of fishes, Vol. 2. Acad. Pr. N.Y. 229 - 269.

BAERENDS,G.P. (1971). The ethological analysis of fish behaviour. In W.S. Hoar and D.J. Randall (eds.), Fish physiology: Environmental relations and behaviour,Vol. 4, Acad. Pr. N.Y. 279 -370.

BAERENDS, G.P. and BAERENDS VAN ROON, J.M. (1950). An intro. to the study of the ethology of cichlid fishes. Behav. Suppl. 1, 1 - 243.

BALAGURA, S. and COSCINA,D.V. (1968). Periodicity of food intake as measured by an operant response. Physiol. Behav. 3, 641 - 643.

BALAGURA, S. and COSCINA, D.V. (1969). Influences of gastro-intestinal loads on meal eating patterns. J. Comp. Physiol. Psychol. 69, 101 - 106.

BALAGURA, S. and DAVENPORT, L.D. (1970). Feeding patterns of normal and ventromedial hypothalmic lesioned male and female rats. J. Comp. Physiol. Psychol. 71, 357 - 364.

BARLOW, G.W. (1962). Ethology of the Asian teleost Badis badis. 111. Aggressive behaviour. Z. Tierpsychol. 19, 29-55.

BASTOCK, M., MORRIS, D. and MOYNIHAN, M.(1953). Some comments on conflict and thwarting in animals. Behav. 6, 66 - 84.

BEACH, F.A. (1950). The Snark was a Boozum. Am. Psychol. 5, 115 - 124.

BERG, L.S. (1958). System der Rezenten und fossilen Fischartigen und Fische. Veb.. Deutscher Verlag der Wissenschaften, Berlin, 310pp.

BINDRA,D. (1969). The interrelated mechanisms of reinforcement and motivation and the nature of their influence on response. In Nebraska Syposium on Motivation, W.J. Arnold and D. Levine (eds.) 1 - 33. Univ. Nebraska Pr. Lincoln.

BLASS, E.M. and HALL, W.G. (1976). Drinking termination: Interactions among hydrational, orogastric and behavioural controls in rats. Psychol. Rev. 83, 356 - 374.

BLURTON JONES, N.G. (1958/59). Experiments of the causation of threat postures of Canada geese. Rep. Wildfowl Trust 1960, 46 - 52.

BLURTON JONES, N.G. (1968). Observations and experiments on the causation of threat behaviour in the great tit (Parus major). Anim.Behav. Monogr. 1, 2.

BOLLES, R.C. (1958). The usefullness of the drive condept. In M.R. Jones (ed.) Nebraska Symposium on Motivation : 1958, Univ. Nebraska Pr. Lincoln.

BOLLES,R.C. (1970). Species-specific defense reactions and avoidance learning. Psychol. Rev. 77(1), 32 - 48.

*

BOLS, R.J. (1976) Factors influencing the reinforcing value of aggressive display in the Siamese fighting fish, Betta splendens. Unpubl. Doct. diss. Univ. of Toronto.

BOLS, R.J.(1977). Display reinforcement in the Siamese fighting fish, Betta splendens: Aggressive motivation or curiosity? J.Comp. Physiol. Psychol. 91, 233 - 244.

BOUSFIELD, W.A. (1933). Certain quantitative aspects of the feeding behaviour of cats. J. Gen. Psychol. 8 446 - 454.

BRADDOCK, J.C. and BRADDOCK, Z.I. (1955). Aggressive behaviour among females of the Siamese fighting fish, Betta splendens. Physiol. Zool. 28, 152 - 172.

BRADDOCK, J.C. and BRADDOCK Z.I. (1959). The development of nest building behaviour in the Siamese fighting fish, Betta splendens (Alstr). Anat. Rec. 137(3), 343.

*BOLLES, R.C. (1975). Theory of motivation. 2nd edn. N.Y.: Harper and Row.

BREDER, C.M. (1926). The locomotion of fishes. Zoologica 4, 159 -297.

BRELAND, K. and BRELAND, M. (1961). The misbehaviour of organisms. Am. Psychologist 16, 681 - 684.

BRUCE, R.H. (1977). An experimental investigation of the thirst drive in rats with especial reference to the goal-gradient hypothesis. J. General Psychol. 17, 49 - 60.

CARLISLE, H.J. (1969). Effect of fixed ratio thermal reinforcement on thermoregulatory behaviour. Physiol. and Behav. 4, 23 - 28.

CARLISLE, H.J. (1970). Intermittent heat as a reinforcer for rats in the cold. Phys. and Behav. 5, 861 - 866.

CARYL, P.G. (1979). Communication by agonistic displays: What can games theory contribute to ethology? Behav. 68, 136 - 169.

CHANTRY, D. (1978). Short term changes in responsiveness to models in Betta splendens. An. learning and Behav. 6(4), 469 - 471.

CLAYTON, F.L. and HINDE, R.A. (1968). The habituation and recovery of aggressive display in Betta splendens. Behav. 30, 96 - 106.

COLLier, G. and JENNINGS, W. (1969). Work as a determinant of instrumental performance. J. Comp. Physiol. Psychol. 68, 659 - 662.

COLLIER, G., HIRSCH,E. and HAMLIN,P. (1972). Ecological determinants of reinforcement in the rat. Physiol. and Behav. 9, 705 - 716.

COLLIER, G.H., KANAREK, R., HIRSCH, E. and MARWINE, A. (1976). Environmental determinants of feeding behaviour, or how to turn a rat into a tiger. In M.H. Seigeland H.P. Zeigler (eds.), Psychological Research. The inside story.

COX, D.R. and LEWIS, P.A.W. (1966). The statistical analysis of series of events.John Wiley, N.Y.

CRAIG, W. (1918). Appetites and Aversions as constituents of instincts. Biol. Bull. Mar. Biol. Lab. Hole, 34, 91 - 108.

CRESPI, L.P. (1942). Quantitative variation of incentive and performance in the white rat. Am. J. Psychol. 55,467 - 517.

CRESPI, L.P. (1944). Amount of reinforcement and level of performance. Psychol. Rev. 51, 341 - 357.

DALTON, D.C. (1965). Dilution of diet and food intake in the mouse. Nature, 205, 807.

DARLINGTON, P.J. (1957). Zoogeography. John Wiley, N.Y. 675 pp.

DAVIES, R.F. (1977). Long- and short- term regulation of feeding patterns in the rat. J. Comp. Physiol. Psychol. 91,574-585.

DE BRUIN, J.P.C. (1977). Telencephalic functions in the behaviour of the Siamese fighting fish, Betta splendens Regan (Pisces, Anabantidae). Unpubl. Ph. D. dissertation, University of Leiden.

DELUTY, M.Z. (1976). Excitatory and inhibitory effects of free reinforcers. Anim. Learning and Behav. 4(4), 436 - 440.

DE NOBLE, V. and CAPLAN, M. (1977). Enhanced response acceleration suppression produced by response-independent food presentations in rats with septal lesions. J. Comp. Physiol. Psychol. 91, 107 - 119.

DEUTSCH, J.A. and HOWARTH, C.I. (1963). Some tests of a theory of intracranial self-stimulation. Psychological Rev. 70, 444 - 460.

DORE, F.,LE FEBVRE, L. and DUCHARME, R. (1978). Threat display in Betta splendens: effect of water condition and type of agonistic stimulation. Anim. Behav. 26, 738 - 745.

DOW, M. EWING, A.W. and SUTHERLAND,I. (1976). Studies on the behaviour of cyprinodont fish, 111. The temporal patterning of aggression in Aphyosemionstriatum (Boulanger). Behav. 59.

DUNCAN, I.J.W., DUNCAN, A.R., HUGHES,B.O. and WOOD- GUSH, D.G.M. (1970). The patterns of food intake in female brown leghorn fowls as recorded in a Skinner box. Anim. Behav. 18, 245 - 255.

DYKGRAAF, S. (1933). Untersuchungen uber die Funktion der Seitenorgane an Fischen. Z. vergl. Physiol. 20, 162 - 214.

EISERER, L.A. (1978). Effects of food primes on the operant behaviour of nondeprived rats. Anim. learning and Behav. 6(3), 308 - 312.

ESTES, W.K. (1950). Towards a statistical theory of learning. Psychol. Rev. 57, 94 - 107.

FABRY, P. (1969). Feeding pattern and nutritional adaptations. London: Butterworths.

FANTINO, E., WEIGELE,S., LANCY, D. (1972). Aggressive display in the Siamese fighting fish (Betta splendens). Learning and Motivn. 3, 457 - 468.

FELTON, M, and Lyon, D.O. (1966). The post-reinforcement pause. J. Exp. Anal. Behav. 9, 131 - 134.

FIGLER, M.H. (1972). The relation between the eliciting stimulus strength and habituation of the threat display in male Siamese fighting fish, Betta splendens. Behav. 42, 63 - 96.

FIGLER, M.H., KLEIN, R.M., RADFORD, R.B. (1973). The effects of chlordiazepoxide (Librium) on the attack behaviour of male Siamese fighting fish, Betta splendens. Proc. Ann. Convent. Amer. Psychol. Assn. 8, 1027-1028.

FISHER, R.A. (1951). The design of experiments. Oliver and Boyd, 6th edn.

FISHER, R.A. and YATES, F. (1953). Statistical tables for Biological Agricultural and Medical research. Oliver and Boyd, 4th edn.

FORSELIUS, S. (1957). Studies of Anabantid fishes. Zool. Bid. Upps. 32, 93 - 597.

GALLAGHER, J.E., HERZ, M.J. and PEEKE, H.V.S. (1972). Habituation of aggression: the effects of visual social stimuli on behaviour between adjacently territorial convict cichlids (Cichlasoma nigrofasciatum). Behav. Biol. 3, 359 - 368.

GALLISTEL, C.R. (1973). Self-stimulation: the neurophysiology of reward and motivation. In The physiological basis of memory (J.A. Deutsch, ed.) pp. 175 - 267. N.Y.: Academic Press.

GIBSON, W.E., REID, L.D., SAKAI, M. and PORTER, P.B. (1965). Intracranial reinforcement compared with sugar water reinforcement. Science, 148, 1357 - 1359.

GLICKMAN, S.E. (1973). Responses and Reinforcement. In Constraints on learning (R.A. Hinde and J. Stevenson-Hinde, eds.)London: Academic Press, pp207 - 241.

GOLDSTEIN, S.R. (1967). Mirror image as a reinforcer in Siamese fighting fish: A repetition with additional controls. Psychon. sc. 7(9), 331 - 332.

GOODRICH, H.B. and TAYLOR, H.C. (1934). Breeding reactions in Betta splendens. Copeia, 4, 165 - 166.

GOODRICH, K.P. (1960). Running speed and drinking rate as functions of sucrose concentration and amount of consummatory activity J. Comp. Physiol. Psychol. 53, 245 - 250.

GRABOWSKI, J.G. and THOMPSON, T. (1968). Effects of visual reinforcement duration and fixed ratio schedules an operant behaviour of Siamese fighting fish. Paper to San Francisco Am. Psychol. Assn.cited in Hogan and Roper, 1978.

GREENBERG, B. (1947). Some relationships between territory social hierarchy and leadership in the green sunfish (Lepomis cyanellus). Physiol. Zool. 20(3), 267 - 298.

GUILFORD, J.P. (1973). Fundamental statistics in psychology and education. 5th edn. Tokyo: McGraw-Hill Kogakusha.

GUTHRIE, E.R. (1935). Operant conditioning,extinction and periodic reinforcement in relation to concentration of sucrose used as a reinforcing agent. J. Exp. Psychol. 46, 213 - 224.

HAMILTON, C.R. and BROBECK, J.R. (1964). Hypothalamic hyperphagia in the monkey. J. Comp. Physiol. Psychol. 57, 271 - 278.

HALL, D.D. (1965). An ethological study of three species of Anabantoid fishes (Pisces, Belontidae). Unpubl. Ph.D.Thesis, Oklahoma State University.

HEBB, D.O. (1955). Drives and the C.N.S. (conceptual nervous system). Psychol. Rev. 62, 243 - 254.

HEILIGENBERG, W. (1964). Ein Versuch zur ganzheitsbezogenen Analyse des Instinktverhaltens eines Fisches (Pelmatochromis subocellatus kribensis Boul., Cichlidae). Z. Tierpsychol. 21, 1 - 52.

HEILIGENBERG, W. (1965). The effect of external stimuli on the attack readiness of a cichlid fish. Z. vergl. Physiol. 49, 459 - 464.

HEILIGENBERG, W. and KRAMER, U. (1972). Aggressiveness as a function of external stimulation. J. Comp. Physiol. 77 332 - 340.

HEILIGENBERG, W., KRAMER, U. and SCHULZ, V. (1972). The angular orientation of the black eye-bar in Haplochromis burtoni (Cichlidae: Pisces) and its relevance to aggressivity. Z. vergl. Physiol. 76, 168 -176.

HEILIGENBERG, W. (1974). Processes governing behavioural states of readiness. In D. McFarland (ed.) Motivational control systems analysis. London: Academic Press.

HILGARD, E.R. and MARQUIS, D.G. (1961). Conditioning and learning. Revised by Kimble, L.A., London: Methuen.

HINDE, R.A. (1955/1956). A comparative study of the courtship of certain finches (Fringillidae) Ibis, 97, 706 - 754, 1 - 23.

HINDE, R.A. (1956). Ethological models and the concept of drive. Brit. J. Philos. Sci. 6, 321.

HINDE, R.A.(1959). Unitary drives. Anim. Behav. 7, 130 - 141.

HINDE, R.A. (1970). Animal behaviour: A synthesis of ethology and comparative psychology. 2nd edn. Tokyo: McGraw-Hill Kogakusha.

HIRSCH, E.(1973). Some determinants of intake and patterns of feeding in the Guinea Pig. Physiol. and Behav. 12, 239 - 249.

HIRSCH and COLLIER, G. (1974). The ecological determinants of reinforcement in the Guinea Pig. Physiol. and Behav. 12, 239 - 249.

HIRSCH, E., DUBROSE, C. and JACOBS, H.L. (1978). Dietary control of food intake in cats. Physiol. Behav. 20. 287-295.

HOGAN, J.A. (1961). Motivational aspects of instinctive behaviour in Betta splendens. Unpubl. Ph. D. thesis, Harvard Univ., Cambridge, Mass.

HOGAN, J.A. (1967). Fighting and reinforcement in the Siamese fighting fish (Betta splendens). J. Comp. Physiol.Psychol. 64, 356 - 389.

HOGAN, J.A. (1974). On the choice between eating and aggressive display in the Siamese fighting fish, Betta splendens. Learning and Motivation, 5, 273 - 287.

HOGAN J.A. (1978). The control of operant responding for feeding and fighting by deprivation and preexposure in the Siamese fighting fish (Betta splendens). Cited as in preparation by Hogan and Roper, 1978.

*

HOGAN, J.A., KLEIST, S. and HUTCHINGS, C.S.L. (1970). Display and food as reinforcers in the Siamese fighting fish (Betta splendens). J. Comp. Physiol. Psychol, 70, 351-357.

HOGAN, J.A. and ROPER, T.J. (1978). A comparison of the properties of different reinforcers. In Advances in the study of beha viour, 8, 155 - 255.

HULL, C.L. (1943). Principles of behaviour. New York: Appleton-Century-Crofts.

HUNSICKER, J.P. and REID, L.D. (1974). "Priming effect" in conventionally reinforced rats. J. Comp. Physiol. Psychol. 87, 618 - 621.

HUTT, P.J. (1954). Rate of bar pressing as a functiin of quality and quantity of food reward. J. Comp. Physiol. Psychol. 47, 235 - 239.

IERSEL, J.J.A. VAN (1953). An analysis of male three-spined stickleback (Gasterosteus aculeatus L.) Behav. Suppl. 3, 1 - 159.

JOHNSON. R.N. and JOHNSTON, L.D. (1973). Intra and inter-specific social and aggressive behaviour in the Siamese fighting fish Betta splendens. Anim. Behav. 21, 665 - 672.

Kanarek, R.B. (1975). Availability and caloric density of the diet as determinants of meal patterns in cats. Physiol. and Behav. 15, 611 - 618.

KEESEY, R.E. and KLING, J.W. (1961). Amount of reinforcement and and free-operant responding. J. Exp. anal. Behav. 4, 125 - 132.

KENNEY, N.J. and MOOK, D.G. (1974). Effects of ovariectomy on meal patterns in the albino rat. J. Comp. Physiol. Psychol. 87, 302 - 309.

KILLEEN, P. (1969). Reinforcement frequency and contingency as factors in fixed ratio behaviour. J. Exp. Anal. Behav. 12, 391 - 395.

KING, B.M. and GASTON, M.G. (1976). Factors influencing the hunger and thirst motivated behaviour of hypothalamic hyperphagic rats. Physiol. Behav. 16, 33 - 41.

KINTSCH, W. (1962). Runway performance as a function of drive strength and magnitude of reinforcement. J. Comp. Physiol. Psychol. 55, 882 - 887.

KISSILEFF, H.R. (1970). Free FEEding in normal and "recovered lateral" rats monitored by a pellet detecting eatometer. Physiol. Behav. 5, 163 - 173.

* Hogan, J.A. and Bols, R.J. (1980). Priming of aggressive motivation in Betta splendens. Anim. Behav. 28 (1), 135-142.

KLEIN, R.M., FIGLER, M.H. and PEEKE, H.V.S. (1976). Modification of consummatory (attack) behaviour resulting from prior habituation of appetite (threat) components of the agonistic sequence in male Betta splendens (Pisces, Belontidae). Behav. 58, 1 - 25.

KLING, J.W. and SCHRIER (1971). Positive reinforcement. In Woodworth and Schlosberg's Experimental Psychology (J.W. Kling and L.A. Riggs, eds.) pp. 615 - 702.

KNARR, F.A. and COLLIER, G. (1962). Taste and consummatory activity in amount and gradient of reinforcement functions. J. Exp. Psychol. 63, 579 - 588.

KONORSKI, J. (1967). Inte grative activity of the Brain. Chicago Univ. of Chicago Press.

KORTLANDT, A. (1940). Eine Ubersicht der angeborenen Verhaltensweisen des Mit-teleuropaischen Kormorans (Phalacrocorax carbo sinensis). Arch. neerl. Zool. 14, 401 - 442.

KRAELING, D. (1961). Analyses of amount of reward as a variable in learning. J. Comp. Physiol. Psychol. 54, 560 - 565.

KRUIZT, J.P. (1964). Ontological social behaviour in Burmese red junglefowl (Gallus, gallus spadiceus Bomaterre). Behav. suppl. 12.

KUHME, V.W. (1961). Verhaltensstudien am maulbrütenden (Betta anabantoides Bleeker) und am nestbauenden Kampffisch (Betta splendens Regan). Z. Tierpsychol. 18, 33 - 55.

KUTSCHER, C.L. (1969). Species differences in the interaction of feeding and drinking. Ann. N.Y. Acad. Sci., 157, 539 - 552.

LASHLEY, K.S. (1929). Learning: 1. Nervous mechanisms in learning. In C. Murchison (Ed.) The foundations of experimental psychology. Worcester, Mass.: Clark Univ. Press.

LE MAGNEN, J. and TALLON, S. (1966). La periodicite spontane de la prise d'aliments ad libitum du rat blanc. J. Physiol. Paris, 58, 323 - 349.

LE MAGNEN, J. and DEVOS, M. (1970). Metabolic correlates of meal onset in the free food intake of rats. Physiol. Behav. 5, 805 - 814.

LANDLESS, P.J. (1974). Demand feeding and growth in Salmonids. Unpubl. Ph. D. thesis, University of Stirling.

LANDLESS, P.J. (1975). Demand-feeding behaviour in trout. Aquaculture. 7, 11-25.

LARUE, C.G. and LE MAGNEN, J.(1972). The olfactory control of meal patterns in rats. Physiol. Behav. 9, 817 - 822.

LAUDIEN, H. (1965). Untersuchungen uber das Kampfverhalten der Mannchen von Betta splendens Regan (Anabantidae, Pisces). Z. wiss. Zool. 172, 134 - 178

LEA, S.and ROPER, T.J. (1977). Demand for food on fixed ratio schedules as a function of the quality of concurrently available reinforcement. J.Exp. Anal. Behav. 27.

LEEMING, F.C(19 8). Response rate as a function of magnitude and schedule of heat reinforcement. J. Exp. Psychol. 76, 74 - 77.

LEONG, C. (1969). The quantitative effect of releasers on the attack readiness of the fish Haplochromis burtoni (Cichlidae: pisces). Z. vergl. Physiol. 65, 29 - 50.

LEVITSKY, D.A. and COLLIER,G. (1968). Effects of diet and deprivation on meal eating behaviour in rats. Physiol. Behav. 3, 137 - 140.

LEVITSKY, D.A. (1974). Feeding conditions and intermeal relationships. Physiol. Behav. 3, 137 - 140.

LEVY, N. and SEWARD,J.P. (1969). Frustration and homogeneity of rewards in the double runway. J. Exp. Psychol. 81, 460-463.

LIEM, K.F. (1963). The comparative osteology and phylogeny of the Anabantoidei (Teleostei, Pisces). Univ. of Ill. Press, Urbana. 149pp.

LISSMANN, H.W. (1933). Die Umwelt des Kampffisches (Betta splendens Regan). Z. vergl. Physiol. 18, 65 - 111.

LOBB, M.L. and McCAIN, G. (1976). Procedurally related differences in the aggressive behaviour of Betta splendens. Anim. Learning and Behav. 4(4). 367 - 373.

LOGAN, F.A. (1960). Incentive: How the conditions of reinforcement affect the performance of rats. New Haven: Yale Univ. Press.

LOGAN, F.A. (1964). The free behaviour situation. In Nebraska Symposium on Motivation, 1964 (D. Levine, ed.) Univ. of Nebraska Press, Lincoln.

LOWE, C., DAVEY, G.C.L. and HARZEN (1974). Effects of reinforcement magnitude on interval and ratio schedules. J. Exp. Anal. Behav. 22, 553 - 560.

MILLER, N.E. (1951). Learnable drives and rewards. In S.S.Stevens (ed.) Handbook of experimental psychology. New York: Wiley.

MILLER, R.J. (1964). Studies on the social behaviour of the blue Gourami, Trichogaster trichopterus (Pisces, Belontiidae). Copeia 3, 469 -496.

MILLER, R.J. and HALL, D.D. (1968). A quantitative description and analysis of courtship and reproductive behaviour in the Anabantoid fish Trichogaster leeri (Bleeker). Behav. 32, 83 - 149.

MORGAN, C.T. and FIELDS, P.E. (1938). The effect of variable preliminary feeding upon the rats' speed - of - locomotion. Journal of Comparative Psychology, 331- 348.

MORRIS, D. (1957). "Typical intensity" and its relation to the problem of ritualization. Behav. 11, 1 - 22.

MOYNIHAN, M. (1955). Some aspects of reproductive behaviour in the black-headed gull (Larus ridibundus L.) and related species. Behav. Suppl. 4, 1 - 201.

MOYNIHAN, M. (1958). Notes on the behaviour of some North American gulls: II Non-aerial hostile behaviour of adults. Behav. 13, 312 - 329.

MYRBERG, A.A. (1965). A descriptive analysis of the behaviour on the African cichlid fish, Pelmatochromis guentheri (sauvage). Anim. Behav. 13, 312 - 329.

McCleary, R.H. (1977). On satiation curves. Anim. Behav. 25, 1005 - 1015.

MacDONALD, G.E. and DE TOLEDO, L. (1974). Partial reinforcement effects and type of reward. Learning and Motivation 5, 288 - 298.

McFARLAND, D.J. (1965). An experimental and physiological analysis of irrelevant behaviour in the Barbary dove. Unpubl. Ph. D. thesis, Univ. of Oxford.

McFARLAND, D.J(1965). Control theory applied to the control of feeding in the Barbary dove. Anim. Behav. 13, 478-492.

McFARLAND D.J.(1966). On the causal and functional significance of displacement activities. Z. Tierpsychol. 23, 217 - 235.

McFARLAND, D.J. (1971). Feedback mechanisms in animal behaviour. London and New York: Academic Press.

McFARLAND, D.J. (1976). Form and function in the temporal organization of behaviour. In R.A. Hinde and P.P.G. Bateson, eds. Growing points in ethology, Cambridge Univ. Press.

McFARLAND, D.J. and LLOYD, I.H. (1973). Time shared feeding and drinking. Qtly. J. Exp. Psychol.25, 48 - 61.

McFARLAND, D.J. and McFARLAND, F.J. (1968), Dynamic ana sis of an avian drinking response. Med. Biol. Engng. 6, 659 - 668.

MacKINTOSH, N.J.(1974) The psychology of animal learning. London and New York: Academic press.

MacLEOD. H.A. (1978). Control of feeding patterns in the Barbary dove (Streptopelia risoria). Unpubl. Ph. D. thesis, University of Edinburgh.

NELSON, K. (1964). The temporal patterning of courtship behaviour in the Glandulo-caudine fishes (Ostariophysi, Characidae). Behav. 24, 90 - 146.

Neuringer, A.J. (1967). Effects of reinforcement magnitude on choice and rate of responding. J. Exp. Anal. Behav.10, 417 - 427.

Olds, J. (1956). Runway and maze behaviour controlled by basomedial forebrain stimulation in the rat. J. Comp. Physiol . Psychol.51, 320 - 324.

Olds, J. and MILNER, P.(1954). Positive reinforcement produced by electrical stimulation of the septal area and other regions of the rat brain. J. Comp. Physiol. Psychol. 47, 419 - 427.

OLEY, N.N. and SLOTNICK, B.M. (1970). Nesting material as a reinforcer for operant behaviour in the rat. Psychon. Sc. 21,41 - 43.

OWENS, J.B. and RIDGEMAN, W.J. (1968). Further studies of the effect of dietary energy content on the voluntary intake of pigs. Animal prod. 10, 85 - 94.

PANKSEPP, J.(1973). Reanalysis of feeding patterns in the rat. J. Comp. Physiol. Psychol. 82, 78 - 94.

PANKSEPP, J. and TROWILL, J.A. (1967). Atraoral self injection: The stimulation of self-stimulation phenomena with a conventional reward. Psychon. Sc. 9, 407 - 408.

PAVLOV. I.P. (1906). The scientific investigation of the psychical faculties or processes in the higher animals. The Lancet, 2, 911 - 915.

PEEKE, H.V.S. and PEEKE, S.C. (1970). Habituation of conspecific aggressive responses in the Siamese fighting fish (Betta splendens). Behav. 36,232 - 245.

PEEKE, H.V.S. and VENO, A. (1973). Stimulus specificity of habituated aggression in the stickleback (Gasterosteus aculeatus). Behav. Biol. 8, 427 - 431.

PEEKE, H.V.S. and VENO, A (1976). Response-independent habituation of territorial aggressionin the 3-spined stickleback (Gasterosteus aculeatus). Z. Tierpsychol. 40, 3 - 58.

PETERSEN, S.A. (1975). Gonadal hormones and feeding behaviour in the mouse. Unpubl. Ph.D. thesis, Univ. of Edinburgh.

PETERSEN, S.A.(1976). The pattern of feeding over the oestrus cycle of the mouse. Anim. Behav. 24, 939 -955.

PICCIOLO, A.B. (1964). Sexual and nest discrimination in Anabantoid fishes of the genera Colisa and Trichogaster. Ecol. Monogr. 34, 53 - 77.

POWELL, R.W. (1969). The effect of reinforcement magnitude upon responding under F - R schedules. J. Exp . Anal. Behav.12, 605 - 608.

PREMACK, D. and KINTSCH, W. (1970). A description of free responding in the rat. Learning and Motivation 11, 321 - 336.

PUBOLS, B.H. Jnr. (1960). Incentive magnitude, learning, and performance in animals. Psychol. Bull. 57, 89 - 115.

QUARTERMAIN, D. and WEBSTER, D. (1968). Extinction following intracranial reward: the effect of delay between acquisition and extinction. Science 159, 1259 - 1260.

RAINWATER, F.L. and MILLER, R.J. (1966). Courtship and reproductive behaviour of the Siamese fighting fish, Betta splendens Regan (Pisces, Belontidae). Proc. Okl. Acad. Sci. 47, 98 - 114.

REGAN, C.T. (1909). The Asiatic fishes of the family Anabantidae. Proc. Zool. Soc. Lond. 785 - 787.

RHOAD, K.D., KALAT, J.W. and KLOPFER,P.H. (1975). Agression and avoidance by Betta splendens toward natural and artificial stimuli. Anim. Learning and Behav. 3(3), 271 - 276.

ROBBINS, D. (1969). Effect of duration of water reinforcement on running behaviour and consummatory activity. J. Comp. Psychol.69, 311 - 316.

ROBERTSON, C.M. and SALE, P.F. (1974). Sexual discrimination in the Siamese fighting fish (Betta splendens Regan). Behav. 54, 1 -25.

ROPER, T.J. (1973a). Nesting material as a reinforcer for female mice. Anim. Behav. 21, 733 - 740.

ROPER, T.J. (1973b). The organization of nest building in female mice. Unpubl. Ph. D. dissertation. Univ. Cambr..

ROPER, T.J. (1975). Nest material as a reinforcer for fixed ratio responding in mice. Learning and Motivation 6, 327 - 343.

ROZIN, P.N. and MAYER, J. (1961). Regulation of food intake in the goldfish. Am. J. Physiol. 201, 968 - 974.

SCHARRER, E.S., SMITH, W. and PALAY, S.L. (1947). Chemical sense and taste in the fishes Prionatus and Trichogaster. J. Comp. Neur. 86, 183 - 198.

SELIGMAN, M.E.P. (1970). On the generality of the laws of learning. Psychol. Rev. 77, 406 - 418.

SEYBERT, J.A. and GERARD. I.C. (1976). Acquisition and extinction effects of partial reinforcement under conditions of thirst motivation. Bull. Psychon. Soc. 8, 590 - 592.

SEYBERT, J.A., GERARD, I.C., LAWRENCE, T., NASH,S.W. and WILLIAMS, C.L. (1976). Effects of schedule and magnitude of reinforcement under conditions of thirst motivation. Learning and Motivation 7, 559 - 570.

SEVENSTER, P. (1961). A causal analysis of a displacement activity (fanning) in Gasterosteus aculeatus. Behav. Suppl. 9, 1 - 170.

SEVENSTER P. (1968). Motivation and learning in sticklebacks. In D. Ingle (ed.) The central nervous system and fish behaviour. Univ. of Chicago Press, Chicago, 233 - 246.

SEVENSTER, P. (1973). Incompatibility of response and reward. In R.A. Hinde and J. Stevenson-Hinde (Eds.) Constraints on learning.London: Academic Press, 265 - 283.

SEWARD, J.P., UYEDA. A. and OLDS, J. (1959). Resistance to extinction following cranial self-stimulation. J.Comp. Phys. Psychol. 52. 294 - 299.

SHANAB, M.E., MELROSE, S. and YOUNG, T. (1975). The partial reinforcement effect sustained through blecks of continuous water reinforcement. Bull. Psychol. Soc. 6, 261 - 264.

SHEFFIELD, F.D., ROBY, T.B. and CAMPBELL, B.A. (1954). Drive reduction vs consummatory behaviour as determinants of reinforcement. J. Comp. Phys. Psychol. 47, 349 - 354.

SHETTLEWORTH, S.J. (1975). Feinforcement and the organization of behaviour in golden hamsters: Hunger, environment and food reinforcement. J. Exp. Psychol: Anim. Behav. Processes 1, 56 - 87.

SIEGEL, S. (1856). Nonparametric statistics for the behavioural sciences. New York: McGraw-Hill.

SILVERMAN, H.J. and ZUCKER, I. (1976). Absence of post-fast food compensation in the Golden hamster (Mesocritus auratus). Phys. Behav. 17, 271 - 285.

SIMPSON, M.J.A. (1968). The display of the Siamese fighting fish, Betta splendens. Anim. Behav. Monogr. 1 (whole issue).

SKINNER, B.F. (1932a). Drives and reflex strength I. J. general Psychol. 6, 22 - 37.

SKINNER, B.F. (1938). The behaviour of organisms, an experimental analysis. New York: Appleton-Century.

SLATER, P.J.B. (1974). The temporal pattern of feeding in the Zebra finch. Anim. Behav. 22, 506 - 515.

SLATER, P.J.B. (1975). Temporal patterning and the causation of bird behaviour. In P. Wright, P.G. Caryl and D.M. Vowles (eds.) Neural and endocrine aspects of behaviour in birds. Proceeding of the 2nd Edinburgh conference, 1974. Amsterdam.

SMART, J.L. (1970). Trial and error behaviour of inbred and F1 hybrid mice. Anim. Behav. 18, 445 - 453.

SMITH, H.N. (1937). The fighting fish of Siam. Nat Hist. 39 264 - 279.

SMITH, H.N. (1945). The freshwater fishes of Siam. Bull. Us. Nat. Hist. Mus. 188, 1 - 622.

SNYDER, H.L. Sácharine concentration and deprivation as determinants of instrumental and consummatory response strengths. J. Exp. Psych. 63, 610 - 615.

SPENCE, K.W. (1945). An experimental test of the continuity and non-continuity theories of discrimination learning. J. Exp. Psychol. 35, 253 - 266.

STEINBACH, G. (1950). Funktionelle und vergleichende Anatomische Untersuchungen uber die Bauchflossen von Trichogaster trichopterus Pallas. Deutsche Zool. Zeitsch.1, 24 - 60.

STEVENSON-HINDE, J. (1973). Constraints on reinforcement. In R.A. Hinde and J. Stevenson-Hinde(eds.)Constraints on learning, pp. 285 - 296. London: Academic Press.

STOKES, A.W. Agonistic behaviour among blue tits at a winter feeding station. Behav. 19, 208 - 218.

TAPP, J.T. (1969), ed. Reinforcement and behaviour. New York: Academic Press.

THACH, J.S. (1970). Modulation of food and water intake by size of fixed ratio. Proc. Ann. Conv. Amer. Psychol. Assn. 5, 755 - 756.

THOMAS, D.W. and MAYER, J. (1968). Meal taking and regulation of food intake by normal and hypothalamic hyperphagic rats. J. Comp. Phys. Psychol. 66, 642 - 653.

THOMPSON, T.I. (1963). Visual reinforcement in Siamese fighting fish. Science 141, 55 - 57.

THOMPSON, T.I. and STURM, T. (1965a). Visual reinforcer colour and operant behaviour in Siamese fighting fish. J. Exp. Anal. Behav. 8, 34-344.

THOMPSON T.I. and STURM, T. (1965b). Classical conditioning of aggressive display in Siamese fighting fish. J. Exp. Anal. Behav. 8, 397 - 403.

THORNDIKE, E.L. (1911). Animal Intelligence. New York: MacMillan.

TINBERGEN, N. (1951). The study of Instinct. London: Oxford University Press.

TINBERGEN, N. (1952). Comparative studies of the behaviour of Gulls (Laridae): A progress report. Behav. 15, 1 - 70.

TINBERGEN, N. (1964). The evolution of signalling devices. In W.M. Etkin (ed.) Social behaviour and organization among vertebrates. Univ. Chicago pp. 206 - 231.

TOATES, F.M. and ARCHER, J.A. (1978). A Comparative review of motivational systems using classical control theory. Anim. Behav. 26 (2), 368 - 380.

TOLMAN, E.C. (1955). Principles of performance. Psychol. Rev. 62, 315 - 325.

TWEEDIE, M.W.F. (1952). Notes on Malayan fresh-water fishes. Bull. Raffles Mus. 24, 63-95.

*

VAAS, K.F.M., SACHLAN,M. and WIRAATMADJA, A. (1953). On the ecology and fisheries of some inland waters along the rivers Ogan and Komering in Southeast Sumatra. Contr. Inl. Fish. Res. Station Bogor 3, 1 - 32.

WATSON, J.B. (1925). Behaviourism. New York: Norton.

WEBER, M. and DE BEAUFORT, L.F. (1922). The fishes of the Indo-Australian archipelago, 4. Brill, Leiden. p.410.

WHITE, R.E.J. (1971). WRATS: A computer compatible system for automatically recording and transcribing behavioural data. Behav. 50, 135 - 161.

* UEXKÜLL, J. von (1934). Streifzüge durch die Umwelten von Tieren und Menschen, Berlin.

WIEPKEMA, P.R. (1969). An ethological analysis of the reproductive behaviour of the Bitterling (Rhodeus amarus Bloch). Arch. neerl. Zool. 14, 103 - 199.

ZEIGLER, H.P. (1964). Displacement activity and motivation theory. A case study in the history of ethology. Psychol. Bull. 61, 362 - 376.

ZEIGLER, H.P., GREEN, H.L. and LEHRER, R.(1971). Patterns of feeding behaviour in the pigeon. J. Comp. Physiol. Psychol. 76, 468 - 477.